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—CYTOKINESIS OF THE
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CYTOKINESIS OF THE POLLEN-MOTHER-CELLS OF CERTAIN DICOTYLEDONS

BY

CLIFFORD HARRISON FARR

Submitted in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in the Faculty of Pure Science
Columbia University

NEW YORK
1916

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CYTOKINESIS OF THE POLLEN-MOTHER-CELLS OF CERTAIN DICOTYLEDONS

CLIFFORD HARRISON FARR
Columbia University

(WITH PLATES 27–29)

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II. REVIEW OF THE LITERATURE

a. Division by cell-plate

Since the notable observations of Strasburger (67*a*) in 1875 on the existence of the so-called cell-plate as a stage in the cytokinesis of higher plants, the assumption has become general that such a structure is universally present in angiosperms, gymnosperms, ferns, and bryophytes. Strasburger already in 1875 discussed the formation of the plate by fusion of thickenings on the central spindle-fibers, its splitting to form the boundaries of the daughter-cells, and the secretion of the cellulose wall or walls between the new daughter-cell boundaries. Strasburger's views have been critically confirmed and enlarged by Treub for the orchids, Mottier for the mother-cells of the lily, Hof for the root-tips of *Ephedra*, *Pteris*, and *Vicia*, Němec for *Allium*, and Timberlake for the root-tips of *Allium* and for the pollen mother-cells of the larch. In addition to this critical work there has appeared in the literature a vast number of more or less casual statements corroborating this interpretation with regard to the cells of various representatives of nearly all groups of the higher plants. Apparently in only one instance has a serious attempt been made to question the universal occurrence of cell-plate formation in the cytokinesis of higher plants, namely, the work of Baranetsky (**4**) in 1880 which has not been recognized as presenting such an exception to this rule, doubtless chiefly because it does not furnish the positive proof of how division may be accomplished without a cell-plate.

On the other hand, it has been just as carefully established that the animal cell divides without the formation of a cell-plate in the equator of the central spindle. Flemming's attempt to homologize the "zwischenkorper" of certain animal cells with the cell-plate of plants has not been generally accepted. The "zwischenkörper" has not been shown to play any part in the formation of the new plasma membranes, whereas this is recognized as a large part of the function and activity of the cell-plate.

Treub (**75***a*) in 1878 presented the first careful observations of cell-division in living material. His findings, in general, agree with those of Strasburger; but in *Epipactis*, he reports, the daughter nuclei travel from one side of the cell to the other, while the cell-plate is being laid down progressively between them. He believed, however, that the cell-plate was of cytoplasmic origin.

In 1887 Went (**79**) for the first time presented the idea that the fibers in the center of the spindle disappear during the growth of the cell-plate. Mottier (**44***a*) in 1897 confirmed Strasburger's observations, using as material the mother-cells of *Lilium* fixed in Flemming's solutions and stained with the safranin, gentian-violet, and orange G combination. It must be remembered that Strasburger's initial work was done on alcoholic material. Mottier studied the process following the heterotypic nuclear division and found that there is "eine auffallende Verdickung der Fäden" in the equatorial region. The mother-cell-wall is shown in his figures to thicken meanwhile to about one twentieth of the diameter of the cell. Strasburger (**67***g*), from his study of *Lilium* and *Alstroemeria*, found that it is the fibers in the center of the spindle in which the equatorial swellings first occur. The elements composing the plate are pulled out and become extremely thin in the middle; and as soon as they break a middle layer appears between them. These equatorial swellings he had (**67***f*) previously designated by the name, "Dermatosomen"; but this term has not been extensively used since then. Hof (**30**) in 1898 stated that the cell-plate formation is accompanied by the shortening of the fibers of the central spindle, but showed no drawings to support this view. Wager (**78**) more recently has figured cell-plates in the root-tips of *Phaseolus*. Davis (**11**) concluded that the fibers involved in the formation of the cell-plates of the spore-mother-cells of *Anthoceros* are not those of the central spindle which remained from karyokinesis; but that they are newly organized in the cytoplasm after the disappearance of the latter. Mottier (**44***b*) in 1900 modified his former opinion as to the origin of the cell-plate in *Lilium*, and after a study of *Dictyota* makes the following statement: "That the cell-plate in the higher plants is formed by a lateral union or fusion of the thickened connecting fibers may be seriously questioned, for in some cases these fibers do not thicken very appreciably in the equatorial region, nor do they lie sufficiently close to one another to enable the slightly thickened middle parts to meet and fuse . . . the conclusion seems justifiable, that the cell-plate is formed by a homogeneous plasma which is conveyed to the cell-plate region and deposited there by the connecting fibers." He presents no new drawings of *Lilium* in support of this interpretation.

The most extensive and satisfactory study of cell-plate formation in the higher plants in recent years is that of Timberlake (**73**) on the pollen-mother-cells of the larch and the root-tips of the onion. The author found that the two types of cells are very similar in their procedure in cell-plate formation; he notes, however, a number of differences which evidently seemed to him of minor importance, but in the light of the following discussion appear to be by no means insignificant. His drawings and photographs present the only adequate attempt since Strasburger's "Zellbildung und Zelltheilung" to arrange a sequence of stages in the formation of the cell-plate. The figures of cell-plates by others are mostly isolated and introduced merely incidentally.

In the onion root-tip Timberlake describes the process in less detail than in *Larix*. He believes that new connecting fibers are formed at the periphery of the spindle, both in the early stages of spindle enlargement and during cell-plate formation. Except for the violet-stained fibers the cytoplasm is homogeneous and without granules. The first indication of equatorial differentiation is in the appearance of an orange-staining zone in that region. With the triple stain this zone stains like the young cell-wall, but it does not take ruthenium red or iron-haematoxylin, so that it is probably of different constitution, though Timberlake believes it is of carbohydrate nature. He likens it to the orange zone in *Saprolegnia*, and the neutral zone in *Fucus*. The spindle fibers become apparently thinner in this orange zone, prior to the appearance of the cell-plate elements, which the writer describes as "thickenings of the spindle-fibers" or "swelling on the fiber." He is unable to find evidence of any movement of cytoplasmic granules toward the equator to form the cell-plate, as suggested by Treub. The cell-plate elements are found sometimes to appear before re-organization of the daughter nuclei.

In the larch the central spindle-fibers are found not to multiply by longitudinal division in the early stages of spindle enlargement, as Strasburger holds. But their apparent increase in number is due to their separation, after being aggregated in bundles by pressure of the chromosomes as they move to the poles. The equatorial thickenings on the fibers are much more pronounced than in the onion root-tip. In addition to them there are granules which are blue with Flemming's triple stain, and are variously distributed within the cell during the anaphases and telophases, sometimes "in rows and sometimes sticking to the connecting fibers." The central spindle-fibers at first thicken near the nuclei, giving the same appearance as the fibers of the onion, which are attenuated at the equator. The fibers of the larch then become of uniform diameter, and lastly thicken at the equator, giving rise to swellings. The process continues until the fibers begin to disappear near the nuclei, that is, shorten. "All of the fibers that form cell-plate elements are completely used up in the growth of the cell-plate." The swellings enlarge, come in contact, and fuse. They do not split before fusing. The central spindle grows peripherally, that is, centrifugally by the addition of fibers. The cell-plate splits in the center and the new wall is secreted (fig. 21). There are thus three processes going on: cell-plate formation, plasma membrane formation, and wall formation. In the larch they are all shown to take place centrifugally, and Strasburger (**67***a*) figured the same condition in *Anthericum* after the heterotypic division. Timberlake believes that the wall formation may occur by the secretion of an unstainable solution, perhaps a carbohydrate, between the two plasma membranes. The phenomenon of the separation of the two plasma membranes is discussed in some detail. Of the process he says: "It is hard to conceive of a layer of protoplasm becoming differentiated into two separate layers similar in all apparent respects to each other."

Studies in physical chemistry since the date of Timberlake's paper, especially in the behavior of colloids, should throw considerable light upon these processes of cell-division. The well-known fact of the crystalloid nature of cell-walls and starch grains made it seem likely that the cell-plate is not of this nature, but is more probably colloidal; and its being visible, both in living and fixed material, would indicate that it is probably a suspensoid. Though probably colloidal, it is not very different either physically or chemically from the rest of the cytoplasm, or a surface boundary would form between them, such as delimits the nucleus; in other words, the cell-plate differs from the plasma membranes to which it gives rise, in that it is apparently permeable to substances in the cytoplasm indiscriminately.

A number of interesting variations from the typical procedure are noted by Timberlake in larch. "Whether the mother-cell divides into four cells which form the pollen grains by successive or simultaneous division depends upon the number of spindle-fibers existing in connection with the first nuclear division. If there are enough fibers to form a cell-plate completely across the cell, successive division results; while if the cell-plate does not reach across the cell it is absorbed into the rest of the protoplasm and the final division takes place simultaneously after the second nuclear division." As noted later, Juel (**35***a*) and Tangl (**70**) have found similar incipient cell-plates in the pollen mother-cells of *Hemerocallis*. Though, in the latter, they may not extend from one side of the mother-cell to the other, they seem to reach a condition of maturity as far as they do develop, and remain suspended in the cytoplasm, not being absorbed, as Timberlake reports for the larch.

b. Cytokinesis in the algae

The algae display a considerable range of variation in their method of cell-division. Strasburger was disposed to regard a number of them as having cell-division by means of a cell-plate; but the evidence, so far presented, is by no means conclusive that the division is as it has been found in the higher plants. However, McAllister (**45**) in his study of so simple a form as *Tetraspora* found a great similarity to the typical seed-plant habit of division.

The cytokinesis of *Oedogonium* has been much studied but without clear results. Strasburger (**67***a*) claims that after the nucleus divides in the center of the cell, something like a cell-plate, consisting among other things of a series of black dots is formed. Tuttle (**77**) and Wisselingh (**83**) have since confirmed Strasburger's observations as to the presence of an equatorial differentiation between the daughter nuclei. In the cell-division of *Spirogyra* there exists a somewhat greater departure from the cell-plate type. Strasburger (**67***a*) early described the centripetal development of a cross-wall in the form of a girdle at the equator of the cylindrical cell. The girdle grows by the deposition of material on its inner edge where starch granules accumulate. The existence of true central spindle fibers running between the two daughter nuclei is still doubtful. In *Cladophora* we have an instance of division of a multinucleate cell without even the semblance of a cell-plate. This was first observed by von Mohl (**43***a*) in his famous pioneer work upon the origin of the cell. In 1854 Pringsheim (**53**) reported the finding of a thin division wall before the centripetal ingrowth is completed; but about twenty years later Strasburger (**67***a*) worked out the details more carefully. There is a ring-like girdle of cell-wall material which grows centripetally across the middle of the cell. As in *Spirogyra* the ring is margined by a circle of dense protoplasm. In *Ulothrix* the same author (**67***a*) presents an example of a uninucleate cell which after karyokinesis forms its cross wall entirely centripetally. There is no doubt an excellent field for research on the cell-division of these filamentous green algae.

In the brown algae several instances have been reported of a division of the protoplast simultaneously across the equator of the cell. This perhaps should not be taken to mean that the cell-division takes place suddenly, but rather that at any one moment the process is at the same stage of development in all parts of the equatorial plane. Strasburger (**67***k*) and more recently Swingle (**68**) have investigated the process in *Sphacelaria.* Swingle finds that cell-division is first indicated by the transverse arrangement of the alveoli in the equatorial plane between the daughter nuclei. A number of granules may appear in this region, and presently a fine line is noticed forming a bridge across the entire cell, or sometimes only across a part. A cellulose wall then appears. The author is unable to relate this to the spindle fibers which are considered insufficient in number, and do not multiply during the processes just described. It is concluded that the process is not dependent upon the activity of the kinoplasm, but, nevertheless, may be under the control of the nuclei.

Mottier (**44***b*) found a similar manner of cell-division in *Dictyota.* Neither Swingle nor Mottier present in figures any stages in the development of the partition. They each give one figure, and supplement this by description. While the latter is valuable, it cannot replace an accurate reproduction of the evidence at hand. Until some one presents an adequate series of stages of the process we must continue to regard their evidence as not entirely convincing. In fact it may even be questioned as to whether we should apply the term cell-plate to these various sorts of formations in the lower plants; it seems desirable rather to restrict the term to that perfectly definite sort of structure that Timberlake and others have described, and which seems to be so prevalent in the higher plants.

Farmer and Williams (**18***a* + *b*) have studied the division of the protoplasm in the oogonia of *Fucus*, where there are eight nuclei, each of which becomes separated at the same time from the others by plasma membranes; that is, there are no divisions of the cytoplasm during the three preceding nuclear divisions. They describe the process as beginning by the elongation of the eight nuclei and the development of polar radiations. The division planes themselves are marked by the accumulation of granules which are repelled equally from all nuclei. These granules fuse into plates which divide the protoplast into its eight respective parts. The authors refer to the process as due to a repulsion of material from the nuclei, but it may as well be considered an ordinary diffusion of material away from the nuclei. It is then essentially like the cell-plate formation in higher plants, except that a central spindle is absent. It will be noted that this is also an instance of simultaneous partition as in *Sphacelaria* and *Dictyota*.

Fucus is not the only alga in which the division of a protoplast into more than two parts has been studied. Strasburger (**67***a*) noticed the quadripartition of the zygospore of *Craterospermum* [*Mougeotia*], by ring-shaped primordia of the cross-walls, that is, by infolding and constriction in a centripetal manner. A more lucid description was given by Berthold (**6**) in 1886 of tetraspore formation in the red alga, *Chylocladia*. Here we have the partition into four spores which are tetrahedrally arranged by "sechs dementsprechend orientirte Membranleisten welche, wie bei *Spirogyra*, allmählich von der Zellperipherie nach innen vordringen." No cell-plate is involved in the process. Unfortunately no figures of the cells in division are given.

c. Cytokinesis in the fungi.

Division by cleavage furrows without the formation of a cell-plate is the common method among the fungi, as Harper has shown in many forms. There is the simple bipartition of a two-nucleate cell, as in the conidiophores of the Erysipheae (**28***a*) the more complex "progressive cleavage" of the multinucleate sporanges, and also of the Mucorineae, etc. (**28***c*). Careful study and search has revealed no evidence of the formation of a partition plane or cell-plate in advance of the cleavage furrow, the only differentiation which takes place, being in certain cases the appearance of a clearer hyaline zone, instead of a dense protoplasm, just in front of the furrow. In the case of *Synchytrium*, Harper (**28***c*) suggests that there are two processes involved in cleavage. "If in *Synchytrium* the nuclei are centers for the formation of kinoplasm, and it proceeds outward from them by diffusion in all directions till it reaches the plasma membrane; this will be correspondingly increased in thickness, and if the mass be decreasing in volume by loss of water and tending to split up like a mass of drying starch, the membrane might perhaps press into the furrows thus formed, so as to become the surface layer of the forming segments."

In the Myxomycetes (**28***f*), Harper finds further evidence of the correlation of loss of water with cell-division. In *Didymium* cell-division is accompanied by an extrusion of cell-sap, "which is initiated and controlled by changes in the spore-plasm." The writer suggests that "If we add to this conception of the nucleus as a center of water retention the further conception, suggested by its relation to cell-plate formation in the higher plants and the ascus, that it is a center for the production of plasma membrane materials, we have two factors which would work in harmony to bring about the process of progressive cleavage described, since the diffusion outward from the nucleus of substances to be used in forming the plasma membrane would again tend to cause the cleavage planes to pass midway between any given pair of nuclei." In his work on *Fuligo* (**28***d*) the same author found that while the cleavage furrows cut midway between two nuclei, the process has no relation to the orientation of the preceding nuclear division figures.

d. Cytokinesis in animals

In the animal kingdom there is considerable variation in the process of cytokinesis, though it hardly displays as wide a range of types as the plant kingdom. In the typical case the cell becomes ellipsoidal and there is a tendency for the two halves, each containing one nucleus and one centrosome, to round up, which is accomplished by a constriction furrow. This is particularly true of some of the small eggs, as those of worms. On the other hand, some eggs with large yolk, as those of the frog, retain their general spherical form, and the furrow is more in the nature of a line of dehiscence. Terni (**71**) has recently published figures which show that amphibian cells may divide either by a broad curved furrow (fig. 26), or a sharp furrow (fig. 25), or a broad furrow with a sharp angle (fig. 40).

How widespread in the animal kingdom this very simple type of cell-division may be is not entirely clear. Such cells as eggs which occur free in the medium, lend themselves much more readily to cell-division studies than do cells of tissues, such as cartilage, muscle, etc. They are also of greater interest from a reproductive standpoint, and hence it is no wonder that most of our knowledge of animal cell-division is based upon the observation of such cells. In the minds of many zoölogists there has not been an adequate distinction between the processes of nuclear and cell-division. Rabl in 1885 published his paper entitled "Ueber Zelltheilung" (**54**), which devotes only two paragraphs to cell-division proper, and over 100 pages to karyokinesis. This simply serves to indicate the place of secondary interest to which cytokinesis had been relegated.

None the less, a vast amount of effort has been expended in attempting to find some equivalent in animal cells of Strasburger's beautiful and clean-cut figures of cell-division in the higher plants. Hofmann (**31**) in 1898 published an excellent review of the literature bearing on the existence of a cell-plate in animals, and adds some interesting observations on hydroids and *Limax*. He deliberately chose animal cells which were imbedded in a matrix having a high coefficient of viscosity and a low coefficient of elasticity, so that the external conditions would closely simulate those of most plants. There can be no doubt that he found equatorial differentiations, as had Flemming and others before him; but whether these should be considered homologous to the cell-plate of the higher plants is not entirely certain. Unfortunately, his preference for the iron-haematoxylin stain makes comparison with the leading botanical investigations difficult. No orange zone is reported such as Timberlake found in the onion. Only one figure of *Limax* and one of *Trutta* show an inflated spindle; whereas many figures of all species studied present an hourglass-shaped spindle. There are only a few cases noted of granules fusing to form a plate, in most instances the granules remaining quite distinguishable. Several cases show a large globular zwischenkorper; and none show a centrifugal splitting of the plate. The present tendency among reputable zoölogists is to avoid the attempt to harmonize the cell-plate in plants with any equatorial differentiation in animal cells; and it seems advisable, at least, to use the term "zwischenkorper" or "diasteme" for such structures in animals, reserving the word "cell-plate" for the higher plants only.

e. Theories of cell-division

Very numerous theories of cell-division and related phenomena have been offered. Perhaps most students have believed that it is an expression of the working of the architectural mechanism of the cell. One school believes that there is a radiating system of organic rays about the centrosome. To this belong: Van Beneden, Boveri, Flemming, Hertwig, Solger, Zimmermann, Heidenhain, and Kostanecki. Von Fick (27) takes exception to this in that it does not take account of the surface relations; and Rhumbler assumes that cell-division is brought about by a combination of surface forces and those of the internal mechanism.

A number of investigators have attempted to place the study on a physico-chemical basis by proposing what have been referred to as the dynamic theories of cell-division. Gallardo (22) reviews the literature up to 1902. Fol in 1873 suggested that the achromatic figure resembles the arrangement of iron filings over a magnet. Soon afterwards Strasburger referred to the resemblance of the spindle to a magnetic field as a peculiar coincidence. A number of workers modeled fields of force to represent mitotic figures in various kinds of media; Giard in 1876 in liquids; Faraday with sulphate of quinine crystals in spirits of turpentine; Gueblard with copper and lead acetates; and Bütschli with gelatin. Errera in 1880 discredited the belief that there are electrical phenomena at work in the cell by experiments with cells of *Tradescantia* dividing in the field of a powerful magnet. He interpreted cell-division as a hydrodynamic process. Fick in 1897 made the suggestion that macroscopic models cannot reproduce microscopic phenomena, since capillarity and other molecular forces are at work in the one but not in the other. Prenant contends that there are two forces: a traction or centripetal force; and a compression or a centrifugal force. Meves discredits the idea of the fibers as representing lines of force on the ground that they often cross; but Wilson affirmed that "the crossing of rays is not necessarily fatal to the assumption of dynamic centers." Gallardo attempts to show how the tilting of the spindle may cause an apparent crossing of fibers which really do not cross. The trained cytologist will, however, hardly accept this as proof that there is no crossing of fibers in the cell. Wilson objects to the dynamic interpretation on the ground that it cannot explain the tripolar figures. Hartog (**29**) has made, perhaps, the most careful attempt to correlate the kinoplasmic fibers with lines of force. He concludes that they are the result of a force which is "analogous to magnetism, and still more to statical electricity." Their behavior is due to their relative conductivity: the fibers, membranes, and chromosomes being of high conductivity.

Still more recently, interesting studies on the chemical changes in the cell incident to cell-division have appeared. Robertson (**55**) suggests that cholin is formed as a by-product about the daughter nuclei, and diffuses in all directions, hence reaching its maximum concentration in the equatorial plane. This causes a diminution in surface tension along the equator and hence the two hemispheres round up against each other. That the cleavage furrow is due to decreased surface tension is also held by Loeb and Lillie; but McClendon and Bütschli contend that it is due to increased surface tension at the equator, which brings about a constriction in that region. McClendon (**46**) has performed many unique experiments in support of his view; these have been otherwise interpreted by Robertson, and the latter has devised experiments to demonstrate the opposite contention; with the result that there is still a question as to which condition does exist.

f. Terminology of cell-division

In spore-mother-cells each nuclear division may be at once followed by cell-division, or cell-division may take place after the four nuclei have been formed. There has been some confusion in the terminology here. Strasburger referred to the latter process at first by the term "simultan" (**67***a*), and later (**67***f*) by the word "Viertheilung." The same writer refers to the process of partition in *Fucus* and *Sphacelaria* as simultaneous, as opposed to progressive. It seems that this term simultaneous should be restricted to the type of cell-division in these brown algae, meaning that the process of division is at the same stage of development in all parts of the division plane. In referring to the two types of division characteristic of spore-mother-cells, Guignard (*26c*) calls them "bipartition successive" and "quadripartition simultanée." I shall refer to them as simply bipartition and quadripartition respectively.

There is also some confusion as to the use of the word "tetrad." Farmer and many zoölogists have applied it to certain chromosomes in diakinesis, while it has also been used by others to refer to the four spores resulting from a single mother cell. The latter use, no doubt, grew out of the fact that these four spores are frequently tetrahedrally arranged; and consequently there comes the question as to whether four spores arranged in a monoplanal rectangle or a rhomb should also be called a tetrad. In view of this confusion and inasmuch as "the four spores" is generally understood as referring to the product of a single mother-cell, it seems more reasonable to restrict the term tetrad solely to the chromosomes.

One more instance of confused terminology might be noted in this connection. The terms, "phragmoplast" and "cell-plate," are used to refer to the same thing. The former is of more common occurrence in the older literature, and its use has been resumed recently by Ernst and Schmidt (15) and others. Inasmuch as the structure in question is transitional, and during its existence the cell is constantly undergoing transformation, it would seem to possess little similarity to such permanent cell-organs as the plastids. Since the term, "phragmoplast," suggests such a relationship, it should probably be abandoned, and the term "cell-plate" alone be retained.

g. Quadripartition in cryptogams

As noted above, the phenomenon of quadripartition occurs in the algae in the germination of the zygospore of *Craterospermum* [*Mougeotia*] and in the formation of the tetraspores of *Chylocladia* and other red algae. Quadripartition has been reported in a number of instances for the bryophytes. Strasburger was the first to do this (67*a*), when in *Pellia* he reported a tetrahedral lobing of the mother-cell, and division by cell-plates following. In the same form Farmer has reported both bipartition (16*c*) and quadripartition (16*d*) by cell-plates with the nuclei tetrahedrally arranged. In *Aneura* [*Riccardia*] (**17**), Farmer and Moore describe a transformation of the mother wall into a quadrilobed structure during reduction. After the heterotypic karyokinesis a wall is formed across the interzonal fibers; after the homoeotypic division the respective lobes are delimited from each other at the center of the original cell, by walls which take up the same position as do soap bubble films when placed in boxes of corresponding form. Ultimately fresh walls are formed around the content of each cell, and the spores separate by the solution of the original walls. Earlier (**16*a***) Farmer had described quadripartition into four tetrahedrally arranged spores in *Pallavicinia* and *Aneura* as taking place only partially by cell-plates, "the cell-walls at their inner angles grow into the cell-cavity," and the spores finally become separated by the appearance of membranes. In *Fossombronia* and *Plagiochasma*, he is uncertain as to the relation of cell-plates to cell-division. He has also reported (**16*d***) quadripartition by cell-plates in *Fegatella* [*Conocephalum*], in which they are in the form of a rhomb, with five connecting spindles instead of six. In all his work Farmer has omitted reference to the mother-cell-wall and fails to show it in most of his drawings.

The conditions which obtain in *Anthoceros* have been more extensively studied and by more investigators. Von Mohl (**43*b***) first described the division by "auf der innern Seite der Zellwandung hervorsprossende Leisten . . . später gegen die Mitte der Zelle zusammenwachsen und sich daselbst vereinigen" (pp. 282, 283). Schlacht (**62**) later (fig. 46) indicated centripetal development of a cell-wall after the cleavage of the content (fig. 41). Hofmeister (**32*b***) found the same procedure and studied it by plasmolyzing the cell-content and observing the projection of the new walls centripetally. He adds the interesting observation that the mother-wall swells during the process of division. Strasburger (**67*a***) in the publication in which he established the predominance of cell-plates in the cell-division of higher plants by multiplying the cases of its occurrence, reports that *Anthoceros* has in its spore formation a tetrahedral quadripartition by cell-plates, followed by a rounding up process. The most recent work upon this genus is that of Davis (**11**). He agrees that the quadripartition is tetrahedral, but notes that the fibers crossing the division-planes are not parallel, but assume varying courses and may anastomose. These he believes are not the spindle fibers but rather that they have arisen after the spindle, resulting from the homoeotypic karyokinesis, has disappeared. In this case the cell-walls are formed in the cytoplasm without reference to the fibers. His figure 26 indicates the development of a cell-plate from the center of the tetranucleate mother-cell outward in three (in all, six) directions toward the mother-wall. This should be described then as neither a centripetal nor a centrifugal development, for the latter terms should be used with respect to the individual spindles, and not to the cell as a whole; it might better be referred to as progressive from one side of the spindle to the other, such as Treub noted in his study of the orchids. In view of the following study it is evident that further investigation of cell-division in the mother-cells of *Anthoceros* should be undertaken.

The mosses have scarcely been studied at all in this respect. Sachs on page 13 of his textbook (**59**) reports tetrahedral quadripartition in the spore-formation of *Funaria*. Hofmeister (**32***b*) shows that the mother-wall of *Phascum* swells to eight times its original thickness, and the cell doubles its diameter during the reduction divisions.

In the ferns several cases of quadripartition have been reported. Calkins (**9**) describes such in *Pteris*, where division occurs tetrahedrally and by cell-plates, but no figures are given of the process. In *Osmunda* a similar instance is given by Smith (**65**). Here the tetrahedral arrangement of the nuclei is said to be brought about by a rotation of the spindles and chromosome aggregates during the homoeotypic karyokinesis, the heterotypic spindle having meanwhile broken down into a granular mass. In *Botrychium* Stevens (**66**) describes a similar dense equatorial plate of cytoplasm following the heterotypic spindle. In this species the nuclei at the time of quadripartition may be arranged either in a tetrad or a rhomb. The division is by cell-plates and the mother cell-wall is not shown to thicken during the process. In *Polypodium*, Russow (**58**) described successive bipartition, the mother-cell-wall swelling in water.

Among the fern allies there is a considerable range of variation in the cytokinesis incident to spore formation. For *Equisetum* Russow (**58**) reported tetrahedral quadripartition, the division of the protoplasm beginning at the center of the mother-cell and proceeding outward. Hofmeister (**32***b*), however, noted that there was successive bipartition and that a plate of granules, or sometimes a ring of granules at the equator preceded the centripetal development of the partition wall. Strasburger (**67***a*), describing the same species, says that there are irregular masses of material heaped up in the equatorial plane. He describes the division as quadripartition by cell-plates, the position of the nuclei being either tetrahedral or monoplanal. The mother-cell-wall is reported to swell when placed in a glycerine solution. His figures (**67***b*) are not entirely convincing that there is a plate and not a row of granules across the equator, and they do not demonstrate a centrifugal partition. In *Psilotum* he (**67***a*) also shows an equatorial accumulation of material at the time of the two successive divisions. In the same form Hofmeister (**32***b*) reports monoplanal quadripartition and mentions a girdle of granules about the equator "ohne dass das Auftreten einer solchen Scheidewand vorausginge." In *Isoetes* Strasburger (**67***a*) reports tetrahedral quadripartition by cell-plates, the fibers crossing and swelling at the equator. In *Marsilea* Russow (**58**) reported tetrahedral quadripartition; and more recently Strasburger (**67***j*) has published quite an extensive paper on *Marsilea* in which he reports quadripartition in both the macrospore and microspore formation. His figures show both a monoplanal and a tetrahedral arrangement of the nuclei in the metaphases of the homoeotypic division. The microspore-mother-wall is shown in the figures to be thickened, but no thickenings of the fibers are shown. Strasburger (**67***d*) has also reported quadripartition in *Lycopodium.*

h. Quadripartition in gymnosperms

In the cycads also the mother-wall thickens during the reduction divisions. In this group, however, division into spores is accomplished by two successive bipartitions. The nuclei may lie either in one plane or in a tetrad, as described by Juránvi (**36**) for *Ceratozamia.* His figures of the first division show constriction furrows accompanied by thickening of the mother-wall. Stages in the second division are not figured. Treub found rather obscure cell-plates in the first division of *Zamia* (**75***b*).

In the larch, as noted above, Timberlake has reported both quadripartition and bipartition (**73**), with a predominance of the latter. Harper (**28***d*) asserts that in the former cases the materials of the spindles of the heterotypic division may be used in the homoeotypic nuclear divisions. Hofmeister (**32***b*) reported centripetal division of the cytoplasm in the spore formation of certain Abietineae, but this has never been confirmed. He also notes the absence of a cell-plate and the swelling of the mother-cell-wall in the divisions in *Pinus*.

i. Pollen-formation in monocotyledons

In the monocotyledons a considerable number of instances of quadripartition have been reported. Mottier (**44***c*) shows it in his figure of the embryo-sac of *Helleborus*, where the nuclei are arranged in a rhomb, with five spindles and upon each a cell-plate. The same investigator gives an interesting figure from the embryo-sac of *Lilium*. The four nuclei at the micropylar end of the sac may be arranged either in one plane or tetrahedrally, the latter condition being shown in the drawing. Cell-plates are formed between each pair of nuclei, and also one on the fibers which extend from the egg into the cytoplasm of the embryo-sac. This is one of the few instances of cell-plate formation on fibers which do not run between nuclei. Others are the embryo-sac of *Ephedra* studied by Strasburger, and the embryo development of *Picea* as shown by Hutchinson (**33**) in his figure 41.

The strong tendency to believe that all cell-division in the higher plants proceeds according to the classic type of Strasburger's central spindle and cell-plate formation has been noted. None-the-less the literature contains some indications that in many cases of quadripartition the process may be a furrowing from the surface inward, quite as in the animal and many lower plant cells. Berthold (**6**) in 1886 wrote (p. 217): "Bei der simultanen Viertheilung der Pollenmutterzellen scheinen bemerkenswerthe Besonderheiten nicht aufzutreten. Die neue Zellplatten bilden sich hier entweder wie gewöhnlich bei den höheren Pflanzen und auch in den Sporemutterzellen von *Anthoceros* und *Isoetes* zuerst frei im Zellraum, um erst nachträglich an die alte Membran sich anzusetzen, oder aber sie dringen von dieser aus, *Cladophora* und *Spirogyra* entsprechend, gegen das Zellinnere vor, wie oben schon erwähnt, in Form dicker, plumper Leisten."

Of cell-division in the pollen-mother-cells of the higher plants von Mohl (**43***c*) as early as 1851 made the following remark: "Eine eigenthümliche Bildungsweise, welche die Theilung der Zellen und die freie Zellbildung verbindet, zeigen die Pollenkörner und die Sporen der höheren Kryptogamen. Die Mutterzelle derselben theilt sich nach vorausgegangener Entwickelung von vier, aus der Theilung eines einzigen Kernes hervorgehenden Zellenkernen und gleichzeitiger Resorption desjenigen Kernes, welcher zu ihrer Entstehung Veranlassung gegeben hat, durch Einfaltung ihres Primordialschlauches und allmählige Ausbildung von Scheidewänden (deren es je nach der relativen Lage der Zellenkerne vier oder sechs sind) in vier Abtheilungen (Naegeli's Specialmutterzellen) oder sie theilt sich zuerst in zwei Abtheilungen, welche sich wieder in je zwei Kammern (Naegeli's Specialmutterzellen zweiten Grades) abtheilen. Hofmeister (**32***a*) in 1861 attempted to distinguish between the monocotyledons and dicotyledons on the ground that the cell-plate in the former is progressively formed from one side of the cell to the other, whereas in the latter, according to von Mohl's observations on the Malvaceae, it develops centripetally. At the same time he reported that quadripartition occurred in *Naias major* and in two species of *Iris*. Later (**32***b*) he placed pollen-mother-cells of *Iris* in water and found that in one-half hour the mother-wall becomes thickened and the protoplast divides by constriction furrows. Dippel in 1869 distinguished between the monocotyledons and dicotyledons on the basis of bipartition and quadripartition in the pollen-mother-cells respectively; and Samuelson (**60**) and others have more recently reiterated this view, noting such exceptions as *Nymphaea* and *Asclepias*.

Guignard has been most active in accumulating evidence that quadripartition occurs in monocotyledons. He first found it in orchids (**26***a*) where cell-plates are formed from a series of granules, and stain a pale violet with haematoxylin. He shows only one figure of the process, and in this the four nuclei lie in one plane and granules but no plates are present in the equators. On the other hand, Hofmeister's (**32***a*) figures of bipartition in *Neottia ovata* and *Orchis Morio* indicate incipient constriction, but are unaccompanied by description. Guignard (**26***c*) very recently has published a note giving a list of monocotyledons in which he has observed quadripartition. This includes three species of *Aloe*, four of *Iris*, two of *Sisyrinchium*, three of *Ixia*, two of *Antholyza*, and one each of *Freesia*, *Haworthia*, *Monbretia*, *Gasteria*, and *Apicra*. He also refers to the literature on the occurrence of quadripartition in monocotyledons and bipartition in the pollen-mother-cells of dicotyledons. He cites as cases of the former the work of Strasburger on two species of *Asphodelus*, and of Tangl, Strasburger, and Juel on *Hemerocallis*, besides referring to his own study of orchids, in all of which, except *Cypripedium*, he found quadripartition. As presenting cases of bipartition in pollen-formation of dicotyledons he mentions the following papers: Strasburger on *Ceratophyllum;* Ernst and Schmidt on *Rafflesia;* Strasburger, Frye, and Gager on *Asclepias;* and Frye and Blodgett on *Apocynum*. As showing intermediate types of partition he refers to the work of Samuelsson on *Anona* and *Aristolochia*, to his own observations on *Magnolia*, and to those of Andrews on *Magnolia* and *Liriodendron*. Guignard has not yet published his study of the cytology of the process, but notes the tetrahedral arrangement in *Sisyrinchium*, and the thickening on the inner surface of the mother-wall at the point of insertion of the partition. The paper very clearly establishes the situation as to quadripartition in the flowering plants.

Hofmeister (**32***b*) in 1867 showed that division in the pollen-mother-cells of *Tradescantia* occurs by cell-plate formation. And Baranetsky (**4**) has since confirmed this. Miyake (**42**) shows a figure (152) of what should probably be interpreted as a cell-plate in this form; and the nuclei lie far apart at the time of its formation. In *Allium* also he figures a cell-plate after the heterotypic karyokinesis with the nuclei far apart. He also reports a cell-plate following the same division in *Galtonia*. Strasburger (**67***a*) had previously shown that two successive bipartitions by cell-plates occur in *Fritillaria*, *Lilium*, *Allium*, and *Anthericum*. His figure of the last-named form shows very well the centrifugal splitting of the cell-plate and the centrifugal formation of the new wall between the new plasma membranes. In *Allium* he claims, as Wimmel (**82**) had previously figured, that the mother-wall enlarges and that the cell-plate after the heterotypic karyokinesis may be accompanied by a constriction, "ein ringformiges Beginnen dieser Zellwand an der Wand der

Mutterzelle." Tschistiakoff (**76**) says of *Epilobium* that the division is by constriction of the plasma membrane, the cell-wall being formed from the periphery inward and from the center outward; that is, a combination of centripetal and centrifugal wall-formation (p. 82).

No careful and complete study of the sequence of stages has been given for any one of these plants. In most instances the evidence consists of an isolated drawing without a description, or a statement with neither description nor drawing to substantiate it. *Lilium* has perhaps been studied more than any other form. In addition to Strasburger's early work, Farmer (**16***b*) in 1895 affirmed that a cell-plate was present after the heterotypic karyokinesis, as did Mottier (**44***a*) a year later. Allen (**1***a*) in 1905 published a figure of a cell-plate in the heterotypic division and says that the same occurs in the homoeotypic mitosis. The nuclei are shown to be far apart during cell-plate formation. Schaffner (**61***a*) a year later also published a single drawing of a cell-plate in the heterotypic division. In his textbook Sachs (**59**) shows successive bipartition in *Funkia*, "a lamella of the cell-wall completely divides the mother-cell. . . . The place where the wall of the mother-cell and the partition-wall meet soon becomes thicker, and the two daughter-cells here become rounded off." Wiegand (**80**) shows a figure of a cell-plate after the heterotypic karyokinesis of *Potamogeton*, the peripheral portion of which is without spindle fibers. Of *Convallaria* he says, "A strong nuclear plate follows the division resulting in a cross wall separating the cell into two hemispherical parts." There may be some question as to whether this is the correct use of the term, nuclear plate. Duggar (**14***b*) gives one figure of a cell-plate in the heterotypic division of *Symplocarpus*, and a similar one of *Peltandra*. For *Trillium* Atkinson (**3**) gives two figures of cell-plates in the heterotypic division. In like manner Schaffner (**61***b*) treats *Agave*. For *Galtonia* Miss Digby (**13***a*) shows a thickened mother-wall and a cell-plate in her figure 72. In figure 81 she shows the homoeotypic division occurring apparently after cytokinesis had taken place in the first division; but in figure 79 there is no indication that cell division had occurred previous to the second division. No discussion of this appears in her paper. Tangl (**70**) in 1882 reported quadripartition with four cell-plates accompanied by an invagination of the mother-wall in *Hemerocallis*, but the same year Strasburger (**67***c*) published the statement that the cell-wall is constructed after the first division in this form. Juel (**35***a*) in 1897 presented a long paper in which he showed that the cell-plates after the heterotypic karyokinesis in *Hemerocallis* are incompletely developed and remain suspended in the cytoplasm. The same writer later (**35***b*) reported ephemeral cell-plates in *Carex* after both the heterotypic and homoeotypic karyokineses. In *Zea Mays* Kuwada (**37**) has reported that after the heterotypic karyokinesis the mother-cell occasionally constricts without the formation of a cell-plate (text-fig. 2); this he associates with a subsequent amitosis and the frequent abortion of the pollen. He found the peculiar constriction in only two preparations. In *Musa* Tischler (**74***d*) describes (p. 637) the daughter cells afterthe heterotypic nuclear division as "durch Plasmamembranen voneinander abgegrenzt." The daughter-cells re-divide several times in various planes, forming either a row, a sphere, a square, a rhomb, etc.

j. Pollen-formation in dicotyledons

The evidence regarding the formation of cell-plates in the pollen-mother-cells of dicotyledons is even more variable and fragmentary, though the authors' statements are frequently very positive. Naegeli (**47**) in 1842 was the first to publish on this point. For *Oenothera* he shows a figure of tetrahedral quadripartition, in which the mother-cell-wall is thickened. He figures a similar condition for *Cucurbita Pepo* and *Bryonia*, in the latter case showing an evident constriction. He describes the process only briefly, "auf der innern Oberflache der Membran sechs vorspringende Leisten; dann plötzlich die Bildung von Scheidewänden, die sich in Centrum berühren." He believes, however, that the dividing layers are of the nature of cell-plates and not ingrowths of the cell-wall, as he attempted to show by plasmolysis.

In 1850 Wimmel (**82**) confirmed the observation of Naegeli on *Oenothera* and added studies on two or three other genera. In *Convolvulus* he found that the division is accomplished by a furrowing and shows a figure of the process. The mother-wall is considerably thickened. In *Momordica Elaterium* he found a successive division, and figures the mother-wall here also as somewhat thickened. In *Althaea rosea* he figures a division by cell-plate with the mother-wall somewhat thickened. Three years later von Mohl (**43***c*) published figures of spore formation in the same plant which indicate a division by constriction sometimes accompanied by a cell-plate and sometimes not.

In 1854 Pringsheim (**53**) prompted by the work of von Mohl, to whom he refers in his preface, presented a study of bipartition and quadripartition in pollen-formation. On page 54 he describes the thickening of the mother-cell-wall by regular layers as in collenchyma formation. In *Althaea* there is a quadripartition, either monoplanal or tetrahedral, which appears first as "Trennungslinien." Division, he says, is, however, accomplished by the ingrowth of the mother-wall, as in the Conferveae. In figure 4, plate IV, there is represented a monoplanal square, with a ridge on the inner surface of each of the four sides of the mother-wall, and a square area in the center. He does not adequately describe this central square. From the following study it will be seen that it is not unlikely that the central square represents a mass of mother-wall material which has followed the constriction furrows toward the center of the tetranucleate cell. In 1865 Rosanoff (**56**) published a couple of figures, 24 and 25, of *Acacia paradoxa* in which are shown successive bipartition, the second division of which is accomplished by constriction, and invagination of the mother-wall at right angles to the first division and beginning first along the periphery on the mother-wall and only after a time becoming apparent on the division wall of the heterotypic mitosis. The author does not discuss the process.

Hofmeister (**32***b*) in 1867 included in his book on the "Pflanzenzelle" certain studies of pollen-formation which have not been followed up by later investigators and seem to have been quite forgotten in the recent tendency to ascribe all division of plant cells to the activity of a cell-plate. However, in the light of the following study and of much evidence which has up to the present remained quite isolated, it seems just to attribute to Hofmeister priority in grasping the real situation as to the pollen formation of dicotyledons. Not only did Hofmeister study *Althaea rosea*, which had received so much attention previously, but he also worked on the Cucurbitaceae and the Passifloreae, in addition to certain monocotyledons and *Anthoceros*. In the dicotyledons he reported a centripetal quadripartition and figured it in *Passi-*

flora. In addition to observing the living material, means were used for studying the wall and protoplast separately. He dissolved the wall by means of sulphuric acid or copper-oxy-ammonia, whereupon he could see the constriction furrows in the plasma membrane independent of the cell-wall. On the other hand he plasmolyzed the cell-content and in this way assured himself that the ridges upon the inner surface of the cell-wall grow centripetally to cut the protoplast into the daughter-cells. As noted above, in *Iris* he induced division by causing the mother-wall to swell in water, but he does not report the repetition of this for any dicotyledons, though he did induce the cell-walls to swell. On page 71 he states that the gelatinization of the cell-wall permits the enlargement of the protoplast. If, however, the inner layers only swell, the cell-content is compressed. In addition to quadripartition he also reports bipartition by cell-plate in *Passiflora.*

Seven years later Sachs (**59**) presented a whole series of figures of quadripartition in the pollen-formation of *Tropaeolum minus.* These are evidently drawn from living material and show various conditions of shrinkage and collapse of the protoplast, which, as will be shown later, do occur in material crushed out under the cover-glass. The drawings show very well the thickened wall, and the centripetal formation of the cross-walls. In his discussion Sachs does not agree exactly with the interpretation of Hofmeister and conceives of quadripartition being brought about by absorption of the heterotypic cell-plate and the reconstruction of it in addition to the formation of other cell-plates after the homoeotypic karyokinesis. He says that quadripartition in *Tropaeolum* occurs by the ingrowth of the mother-cell-wall at its junction with the cell-plates. He, however, does not support this contention by drawings.

Strasburger followed the next year with his famous work on the formation of cell-plates (**67***a* + *b*) in a great many plants, in which he included drawings of what he interpreted as cell-plates in the pollen-formation of *Tropaeolum majus.* This is the most complete series of stages in division of the pollen-mother-cells of any dicotyledon that Strasburger has ever published, his other studies presenting merely single drawings. A careful survey of these drawings of *Tropaeolum* reveal apparently swellings of the spindle fibers at the equator, but the evidence that these form a plate is by no means convincing. When it is remembered that this material was fixed in alcohol, and that Strasburger repeatedly expressed his opinion that the pollen-mother-cells of dicotyledons were very unfavorable material for study, there arises a grave doubt as to whether we are justified in accepting these drawings as final proof of the existence of true cell-plate formation in this species. In his discussion he recognizes an "Einschnürung" of the mother-cell, and a thickening of the wall at the equator in the form of a ridge.

On division in the pollen-formation of other dicotyledons, Strasburger gives a few fragmentary remarks. He noted quadripartition in *Cucumis*, *Delphinium*, *Aconitum*, *Glaucium*, *Althaea*, and *Bryonia*, but gives no figures or descriptions of the process. In his paper on *Asclepias* (**67*h***) in 1901, Strasburger showed a peculiar condition, where successive bipartition of the pollen-mother-cells results in a row of four cells. The mother-wall is not thickened, in fact it is scarcely discernible in the drawing. His only descriptions of the division processes are that they are by cell-plates. The following year he published (**67*i***) his *Ceratophyllum* paper, in which he includes no description of cell-division but only one figure, number 46. The mother-cells appear to be closely packed, and to have very thin walls. A partition apparently results from the heterotypic mitosis. The second division may be either monoplanal or tetrahedral.

A few papers have given rather good evidence of the existence of cell-plates in the mother-cells of dicotyledons. Ernst and Schmidt (**15**) recently found successive bipartition by means of cell-plates in *Rafflesia*. It is stated that the nuclei may be arranged either monoplanally or tetrahedrally. Frye and Blodgett (**21**) in 1905 also reported successive bipartition in the pollen-mother-cells of *Apocynum*. They do not discuss the details of the process, but show that it may result in the four spores being arranged tetrahedrally or monoplanally in a square, rhomb, pyramid, or row. In the drawing of the monoplanal square they suggest the existence of a cell-plate, following the homoeotypic karyokinesis. The mother-wall is not shown to be thickened.

In 1907 Lubimenko and Maige (**40**) described a peculiar division in *Nymphaea* in which a cell-plate is formed after the heterotypic karyokinesis, but disappears before cell-division is accomplished. Their figures indicate a tetrahedral quadripartition; but in only one figure, 54, is a cell-plate indicated, and this after the second nuclear division. The mother-wall in the drawing is about one twenty-second of the diameter of the cell. During exine formation the mother-cell-wall is shown to be much thicker. They explain (p. 450) their omission to figure a series of stages in the cell-plate formation after the homoeotypic division as due to a condensation of the cytoplasm about the nucleus, and the formation of a cell-plate so quickly that the different stages could not be found.

The pollen-formation of *Magnolia* has been investigated by several; and apparently it is of another intermediate type. Guignard (*26b*) found that the heterotypic spindle enlarges by the formation of new fibers. Before it reaches the plasma membrane the fibers become very conspicuous and stain heavily in the equatorial region. A granular plate is not shown to appear in the center, but the fibers are grouped together, leaving clear spaces between them. Soon a ridge appears on the inner surface of the mother-cell-wall, which in optical section resembles a wedge projecting toward the center of the cell. This furrow he likens to those in the cell-division of *Cladophora* and *Spirogyra*. The invaginating ring is heavier than in the latter, and the fibers do not thicken enough to account for its ingrowth. As the ring advances the spindle fibers on either side disappear. It does not regularly at this time continue its growth until cytoplasmic division is complete, but stops when the depth of the furrow is about equal to the breadth of the isthmus or protoplasmic bridge remaining between the two halves of the mother-cell. In a few cases the division is said to be complete. The fibers are reformed across the isthmus after the homoeotypic division, and the cytokinesis previously begun is completed usually slightly before the daughter-cells divide. The second division is said to begin like the first, but is more rapid and continues without interruption. He shows no figures of these later stages, which, in fact, constitute the crucial point in establishing the nature of this division. This work was succeeded in 1901 by that of Andrews (**2**). In the title of his paper he includes both *Magnolia* and *Liriodendron*, and he does not indicate in his drawings from which plants they were taken. He agrees in most particulars with Guignard, except that he states that the first division is completed by the formation of a cell-plate across the isthmus. "The formation of the cell-plate of the second mitosis is about in the same way" (p. 139). His figures show constrictions of the protoplast, but in no case do they indicate the semblance of a cell-plate. The most recent work on *Magnolia* is that of Maneval (**41**). He makes no reference to the work of Guignard, but says that the division is simultaneous, while his figures are not entirely in harmony with this interpretation.

In 1914 also there appeared the paper of Samuelsson on *Anona* and *Aristolochia* (**60**) in which he attempts to establish a relationship between monocotyledons and dicotyledons on the basis of the occurrence of both bipartition and quadripartition of the pollen-mother-cells in these forms. In *Aristolochia* he reports successive bipartition, resulting in a monoplanal square or a pyramidal arrangement of the spores. In *Anona* he figures a monoplanal square in which the mother-cell-wall is in thickness about one fourteenth of the diameter of the cell. As Guignard found in *Magnolia*, he reports for *Anona* that in the telophases of the heterotypic mitosis the division of the cytoplasm begins as an equatorial constriction on the periphery of the cell, which is completed after the homoeotypic karyokinesis. The cytokinesis after the homoeotypic karyokinesis is said to agree completely with the first. He does not refer to a cell-plate in any connection throughout the whole paper. He gives no description of his drawings, which appear to be very poorly reproduced. Shibata and Miyake (**63**) present a similar case in *Houttuynia*, which they consider as associated with the abortion of pollen in that form.

It thus appears that there are a number of dicotyledons which display a type of cell division of the pollen-mother-cells which has been regarded as intermediate between true bipartition and true quadripartition. It is generally recognized, however, that the majority of dicotyledons form their microspores by a quadripartition of the mother-cells; but the details of this process of quadripartition have not been accurately determined, and the data in the literature regarding it is not entirely consistent. Some papers as noted below give evidence of the existence of cell-plates in this cytokinesis, while others indicate that it may be accomplished by furrowing.

In 1898 Lawson (**38**) published in the Proceedings of the California Academy of Sciences a figure, 24, of *Cobaea* which shows a pollen-mother-cell after the homoeotypic karyokinesis with the four nuclei tetrahedrally disposed and not appressed to the plasma membrane, though cytoplasmic division has not yet occurred. The spindles are inflated and the mother-wall is about one thirtieth of the diameter of the cell. There is a concavity of the plasma membrane on one side of the mother-cell, a convexity on another, and the third side is flattened. "Cell-plates are now formed in the usual way" (p. 178). Two years later there (**8**) appeared in the same journal a paper by Miss Byxbee on *Lavatera*. Her figure 24, also of a mother-cell, has four nuclei arranged in a monoplanal rhomb also with the suggestion of five spindles between them. The mother-cell-wall is here about one twenty-second of the diameter of the cell, and there is no indication of the division of the cytoplasm either by cell-plates or by furrows. Here also the statement is made that "cell-plates are formed later on" (p. 69). This is the only reference to cytokinesis in the paper. It is evident that the statements as to cell-plates in both *Cobaea* and *Lavatera* must be regarded as quite unreliable.

Tischler has reported a number of instances of quadripartition in pollen-formation, but has never described the details of the process. In 1906 in connection with his study of sterile *Bryonia* hybrids (**74***a*), he gives a figure, number 7, of a mother-cell in which quadripartition would no doubt occur. But he does not refer to it in the text, nor does the drawing show the mother-cell-wall. In the same year in his study of *Ribes* hybrids (**74***b*), he presents two figures indicating quadripartition, one tetrahedral, the other rhomboidal. In 1908 in further work along this line, he gives a number of similar figures (**74***c*). Number 14 shows the mother-wall thickened to about one fourteenth of the diameter of the cell in *Mirabilis*. Number 19 indicates that bipartition has occurred after the heterotypic division, the mother-wall being about one twentieth of the diameter of the cell. In figure 71 he shows a tetranucleate cell of *Potentilla*, with the mother-wall thickened to one tenth the diameter of the cell. Figures 99 and 100 show a like condition in *Syringa*. Of *Mirabilis* he writes (p. 44), "In nicht wenigen Fällen gelingt aber die Ausbildung der Zellplatte nicht mehr: wir erhalten vierkernige Zellen." This constitutes the only evidence which he gives of having seen cell-plates in any of these forms. Of *Syringa*, Juel (**35***b*) states that there is quadripartition by cell-plates, but gives no figures to show it. In the same way Duggar (**14***a*) refers to *Bignonia*, but his figures do not show cell-plates.

In his paper on reduction in the pollen-mother-cells of dicotyledons, Overton (**51**) presents a figure of *Podophyllum*, number 70, which indicates cell-plate formation after the heterotypic division. The mother-wall is not shown, and the division is not discussed in the paper. Mottier (**44***a*) in his paper on the same subject, based also on *Podophyllum*, shows that cell-division does not always occur after the heterotypic division. He gives two figures after the homoeotypic karyokinesis with the four nuclei arranged in a rhomb, with five spindles connecting them. No cell-plates are shown. By four figures of late stages of the heterotypic division he shows that the spindle fibers of that division disappear in the center and are replaced by a granular plate. In his text he says only, "Die Zellplatte wird in der für *Lilium* zuvor beschriebenen Weise angelegt." We must conclude that in *Podophyllum* an ephemeral cell-plate is formed after the heterotypic division, but the division after the homoeotypic karyokinesis should be further studied.

Wille (**81**) in 1886 presented a paper on the formation of the wall of the pollen grains of 22 different plants, in which are incidentally introduced a number of observations of interest in the present study. He devotes especial attention to the thickening of the mother-wall, which he contends is by intussusception, but gives no evidence that anything more than a swelling or gelatinization actually occurs. The thickened wall is said to be made up of "wasserarme und wasserreiche Schichten," as Naegeli and Strasburger held for starch grains. Though both monocotyledons and dicotyledons were studied, he considers division of the pollen-mother-cell as taking place in all cases by successive bipartition by cell-plates. At the end of this paper Wille reports a number of instances of the formation of pollen grains in other than groups of four, the irregularities ranging from one to fourteen in different species. He also described lobed microspores as occurring along with the normal globular forms.

It appears that in no instance is the evidence conclusive that quadripartition of the pollen-mother-cells of any dicotyledon is effected by means of cell-plates. That some dicotyledons form their microspores by two successive divisions with cell-plate formation, can scarcely be doubted, as is shown in *Asclepias*, *Ceratophyllum*, *Apocynum*, and *Rafflesia*. But it is generally recognized that the majority of pollen-mother-cells of dicotyledons do not divide in this way. The best evidence of quadripartition by cell-plate is that of Strasburger in his work on the alcoholic material of *Tropaeolum*, which has been shown above to be not beyond question. On the other hand there is some evidence that cleavage furrows may be involved in the process. The work of Naegeli, Wimmel, von Mohl, Sachs, and Hofmeister suggest it, though such early work should not be taken as by any means final. Guignard and Samuelsson directly affirm it in *Magnolia* and *Anona* respectively.

There is also a considerable list of additional papers which in one way or another indicate that furrowing may be involved in the division of the pollen-mother-cells. As early as 1880 Baranetsky (**4**) in addition to confirming Strasburger's observations on successive bipartition by cell-plates in the pollen-mother-cells of *Tradescantia*, studied this stage in four different dicotyledons. He shows two figures of *Hesperis matronalis* with incipient furrows along the equator. He does not describe them, but says, "Strasburger gibt an, dass 'in allen Fällen' der Theilung der secundären Kerne die Bildung einer Zellplatte zwischen ihnen vorausgeht. Bei den von mir überhaupt beobachteten Dicotylen: *Pisum sativum*, *Lathyrus odoratus*, *Hesperis matronalis*, *Ipomaea tricolor*, konnte ich diese Angabe nicht bestätigt finden."

Ishikawa (**34**) in his figure, number 11, of *Dahlia* shows a pollen-mother-cell in which four nuclei are tetrahedrally arranged. They do not lie near the plasma membrane, but spindles are shown extending between them without the slightest indication of a cell-plate. At the equator on one side there is a concavity, and the other two sides are flattened. No mother-wall is shown, and the paper contains no discussion of the process.

Osawa (**50*b***) shows several figures of division of the cytoplasm in the pollen-mother-cells of *Taraxacum*. Figure 22 is of a pollen-mother-cell with four nuclei tetrahedrally arranged; no mother-wall is shown. The spindle fibers are thickened at the middle throughout about one half their length. One side of the cell is concave, and two flattened; no cell-plate is shown. In the text he only says "the cell-walls are formed between these four nuclei, producing the normal tetrad." Figure 55 shows an instance of bipartition of the pollen-mother-cell. In *Daphne* he (**50***a*) shows a marked furrow on two sides of the mother-cell, which is about to undergo tetrahedral quadripartition. There are also indications of cell-plates here. The mother-wall is about one ninth of the diameter of the cell.

Rosenberg (**57***a*) shows a schematic drawing, text figure III., of successive bipartition in *Hieracium venosum*. In text figure V. he has a tetranucleate mother-cell which is rectangular, and without a thickened wall. He says (p. 149), "The following division stages correspond with, for instance, those of *Tanacetum* or *Taraxacum*, and the development of the pollen cells does not offer anything extraordinary." In no instance does he show a cell-plate. Of *Drosera* he shows several figures of quadripartition. Figure 22 (**57***b*) shows the four nuclei in one plane in the form of a rhomb, with four spindles of equal size, and a fifth small spindle between the two opposite nuclei which are in closest proximity. No indication of a cell-plate is shown. Figure 21 shows a similar stage with tetrahedral arrangement of the nuclei. In figure 2 the mother-wall is shown much thickened and a cleavage furrow is beginning in the equator at the metaphase of the homeotypic division. No cell-plates are likewise shown here. During the course of my investigation on *Nicotiana* and other forms described below, Levine (**39**) in his studies on the germ cells of *Drosera* observed both bipartition and quadripartition in which the mother-cell-wall is much thinner and more angular, as in *Asclepias*, *Ceratophyllum*, etc. His figures show no broad constriction furrow, and at the stage when partition has apparently just been completed, the appearance is as if the mother-cell had divided by cell-plate formation. *Drosera* is one of the plants in which the four pollen grains thus formed never separate. Whether this has anything to do with the mode of cytokinesis in microspore formation is a problem for further investigation.

In her study of *Parnassia* Miss Pace (**52**) presents a figure, 54, which shows tetrahedral quadripartition with the invagination of the thickened mother-wall along the equators. Fibers are shown crossing the equator, but there is no indication of a cell-plate.

The paper contains no discussion of this peculiar situation. Shoemaker (**64**) in *Hamamelis* shows tetrahedral quadripartition with an incipient furrow in figure 31. The mother-wall is much thickened, and no cell-plate is indicated. Miss Fraser (**20**) in her figure 31 of *Vicia* indicates tetrahedral quadripartition; spindles are shown, but no cell-plates; the plasma membranes are rather indistinct, but there are indications of equatorial cleavage furrows. Miss Digby (**13*b***) in her figure, 42, of *Primula* indicates tetrahedral quadripartition with broad furrows on both sides, which are, however, not exactly equatorial. No cell-plates are shown. In figure 67 the mother-wall is shown to be greatly thickened after the division is complete. She writes, "The cytoplasm between the nuclei constricts," but she makes no reference to the presence or absence of a cell-plate. Miss Nichols (**49**) reports tetrahedral quadripartition, in which the cytoplasm "constricts." Her figure 39 shows such a condition, but there are only two nuclei shown. Gregory (**25**) figures for *Lathyrus* a constriction of the protoplast after the heterotypic division. This he states is accompanied by amitosis and is related to sterility of pollen. He evidently regards it as abnormal, as he says that in the fertile pollen the division is "of the usual type." Cannon (**10**) in his paper on hybrid cotton shows quadripartition in figure 14. In figure 16 he shows division taking place between two nuclei by a broad cleavage furrow; no fibers or cell-plate are shown in the cytoplasm. Of the process he says, "Indentations appear in the periphery of the cytoplasm and midway between the nuclei, which deepen into constrictions, and finally accomplish the separation of the nuclei and the formation of the tetrads." He, however, does not discuss the existence of a cell-plate.

The figure which best indicates quadripartition by cleavage furrows is that of Beer (**5*b***) on *Crepis;* unfortunately this is unaccompanied by description. He reports quadripartition in *Matricaria Chamomilla* and *Crepis taraxacifolia*. Three figures of the latter and one of the former indicate this. In *Crepis* the mother-cell-wall is slightly thickened, and the nuclei are appressed to the plasma membrane before the cleavage furrow is well developed. No cell-plate is shown; but figures 57 and 58 show a constriction at different stages of development. The relation of the mother-wall to the furrow is not shown. Tahara (**69**) in his figure 9 shows that the mother-wall in *Crepis* is about one fourteenth of the diameter of the cell, just before quadripartition occurs. In *Ipomoea* Beer (**5***a*) shows the mother-wall very much thickened after the homoeotypic division. He says that this wall gives a reaction to tests for callose and pectose, but does not discuss the cytokinesis. In *Oenothera* he says the mother-wall dissolves in 1 per cent NaOH only after about 24 hours. It is not soluble in strong phosphoric acid. It stains with Bismarck brown, methylene blue, and fuchsin. He therefore concludes it is a modified form of callose or pectose. He says of division that "Septa are developed which form an extension of the mucilaginous mother-cell-wall." Gates (**23**), however, diagrams a cell-plate in his figure 47, though he does not discuss the process in his paper on *Oenothera*.

III. MATERIAL AND METHODS

The greater part of the work here reported has been done upon the pollen-mother-cells of *Nicotiana Tabacum*. In addition observations were made for comparison upon the pollen-mother-cells of *Primula sinensis*, *Tropaeolum majus*, *Ambrosia artemisiaefolia*, *Chrysanthemum frutescens*, and *Helianthus annuus*. The root-tips of the last-named were also studied and compared with the root-tips of the onion and the pollen-mother-cells of *Larix* and *Lilium*.

Both living and fixed preparations of the pollen-mother-cells were studied. With the exception of the *Ambrosia* material, the flowers were collected from individuals growing in the Columbia University greenhouse. In most cases the stamens were fixed individually to insure good penetration of the reagents; however, in the Compositae it was found more practicable to treat the entire flower.

The material was fixed in Flemming's chromic-acetic-osmic solutions in the weak, medium, and strong proportions. The following reagents were also employed: Merkel's; picro-formol; Wilson's sublimate acetic; and Benda's solution. The strong Flemming's formula was found to be the most satisfactory, and had incidentally the additional advantage of being the same reagent which Timberlake and Mottier used, thus affording means of more direct comparison. The same might be said of Flemming's triple stain. While iron-haematoxylin was also used, it contributed little of value to the study.

Sections were made for the most part five microns thick. In some instances, however, it was found advisable to cut them only three or four microns thick so as to remove all of the superficial material from median sections of the dividing mother-cell.

To Professor R. A. Harper, under whose supervision this study was pursued, are due many thanks for his valuable suggestions and criticism, which are deeply appreciated.

IV. OBSERVATIONS ON LIVING MOTHER-CELLS

The study of living material is without doubt a very valuable method in cytological research. So far as the more obvious facts of cell division are concerned, such studies give unimpeachable data, as is evidenced by the accuracy and suggestiveness of the studies of such early cytologists as Naegeli, Pringsheim, and Hofmeister. Lundegardh and others are certainly pursuing a wise course in devoting a large amount of attention to the living cells.

The chief difficulty in the study of living cells lies in the fact that they can be retained in their normal condition for so short a time. In this respect the students of animal cells are more fortunate, since body-fluids may be used to keep the cells alive almost indefinitely. The pollen-mother-cells of the larch are found to break down within ten or twelve minutes after crushing out the content of the anther into tap water. Even before this time has expired, and often almost immediately, the nucleus appears to enlarge, doubtless due to a decrease in the osmotic pressure of the medium. The introduction of a trace of weak alkali was found to prolong the period of normal appearance to between fifteen and eighteen minutes. The pollen-mother-cells of *Tropaeolum*, *Chrysanthemum*, *Helianthus*, and *Nicotiana* were studied in the living condition. This was attempted with *Primula;* but here the mother-cells were apparently bound together so firmly that the entire content of the pollen-sac remains intact during the process of crushing out, and to separate the cells would involve so much abuse of the protoplast as to make the results of no value. In the other dicotyledons noted, the mother-cells readily wash out separately from the anther as soon as it is cut. In these forms the protoplast retains its natural appearance longer than in the larch. This may perhaps be attributed to the enormously thickened mother-wall. The relative thickness is all the more striking when it is remembered that the mother-cells of the larch have a diameter two or three times that of these dicotyledons. The thickness of the mother-wall in the larch is usually less than one tenth of the diameter of the protoplast; whereas in the other forms it is usually more than one third of the diameter of the protoplast.

In the larch the mother-cells seem to pass through the reduction divisions in about forty-eight hours. The wall thickens slightly during the first division; but those of adjacent cells do not cohere, and they separate readily. The various stages in the divisions can be quite easily identified. The nuclei, chromosomes, and very often the spindle fibers are plainly distinguishable. One of the very evident features is the centrifugally forming cell-plate. The cell-plate can be progressively followed from its incipiency as a little streak in the equator, until it reaches the plasma membrane upon either side. It is frequently attached to the plasma membrane upon one side, while it is as yet incompletely developed upon the other. There is no evidence that the plasma membrane proceeds inward either in the form of a concavity or a sharp furrow to meet the cell-plate, the division of the cytoplasm being apparently entirely a function of the latter. However, after the cell-plate is complete, a sharp furrow does appear at its juncture with the plasma membrane of the mother-cell. The formation of this furrow has been referred to by Strasburger as a rounding-up process. Just what is its relation to cell-division is not entirely clear. In the entire process of cell-division in the broadest sense of the word, there are involved at least four distinct processes: the division of the nucleus, the formation of the cell-plate, the formation of the new plasma membranes, and the formation of the new cross-wall.

In *Nicotiana* the presynaptic mother-cells (FIG. 1) are angular in form, the lateral walls being rectilinear in section, and scarcely, if at all, thickened more than are those of the ordinary vegetative cells. The corners, however, are thickened so as to appear in section somewhat like those in collenchyma tissues, though no signs of laminations, such as Pringsheim reported, can be found either in the living or fixed material. The mother-cells when teased out in a drop of water may be seen at this stage to be rarely isodiametric, but are usually longer in one dimension than in the others.

During synapsis the more or less sharp angles become rounded off, so that the cell approaches more nearly to an ellipsoid or ovoid form. At the same time the mother-wall may be seen in crushed-out material to have developed a considerable thickening at either end of the cell. It is frequently noticeable that the mother-wall is flattened on one side parallel to the longitudinal dimension. This flattening may even be so marked that the central optical section appears triangular, or the apex of the triangle may be truncated. When two cells lie contiguous to each other, their flattened faces, which represent the bases of such triangles, are often seen in living material to lie appressed to each other (FIG. 4); and it is at least suggested that this line of contiguity may mark the plane of the last preceding mitosis. Pairs of mother-cells, in which the protoplasts have completely divided into the microspores, may even be found in this relation (FIG. 14), the mother-wall retaining its original form.

The nucleus is seen to undergo progressive enlargement during the stages of presynapsis and of synapsis proper. Lubimenko and Maige (40) believe that this is carried to the point of bursting of the nuclear membrane. No evidence of the latter phenomenon was observed in the present study. Sometimes the nucleus would swell and burst, thereupon completely collapsing, but this was thought to be due to the abnormal medium in which the cells had been placed.

The wall continues to thicken during synapsis, and upon the advent of diakinesis (FIG. 2) it is thicker on all sides, but is still more markedly so at either end. The nature of the process of thickening of the cell-wall will be discussed under the observations on fixed material. The heterotypic spindle may lie either in the longitudinal axis of the mother-cell (FIG. 21), or transverse to it (FIG. 3). As the homoeotypic division takes place (FIG. 4) the wall becomes quite uniformily thickened on all sides. The homoeotypic spindles are frequently at right angles to each other, though they may be at a much smaller angle. After the reorganization of the daughter nuclei there appear occasionally in the living material a few central spindle fibers; though these are difficult to make out. One instance (FIG. 4) was found in which quite a definite row of granules might be seen in the plane midway between the nuclei. The whole cytoplasm, of course, appears very granular in the living material, and it could not be determined whether the granules in question had any specific relation to division. The failure to find further evidence of these granules after studying a great number of living cells, makes one doubt their relation to cell-division. That such rows of granules might appear in any part of the cell is indicated by the evidence from fixed material presented below.

After the homoeotypic mitosis the protoplast assumes a spherical form within the cell-wall, which conforms to the protoplast on its inner surface, but which may have an outer surface of various forms. It would appear that the mother-cell-wall is of such viscosity as to yield to the pressure due to the cell-turgor, but that is has too high a coefficient of viscosity readily to assume a spherical form itself when freely suspended in water. As Hofmeister suggests, there may be a difference in the viscosity of the inner and outer layers of the wall, so that the one takes the form of the enclosed protoplast, while the other retains some of the effects of the external pressure under which it existed within the pollen-chamber. In other words, the outer portion of the cell-wall has an elasticity which operates against its external form being permanently changed by the application of transitory pressure.

When the daughter nuclei become completely re-organized they withdraw as far as possible from each other in the cell, usually assuming a tetrahedral arrangement. Soon the cell-cavity becomes lobed (FIG. 5). It seems that this is not the consequence of the protrusion of the plasma membrane in the region of each nucleus, as Farmer and Moore (**17**) described for similar cells of *Aneura*; but it appears rather that it is due to furrowing of the plasma membrane along the plane midway between each pair of nuclei. The first indication of the furrowing is to be found in the flattening of the protoplast on four sides, each of which is parallel to the plane of three nuclei, so that the entire protoplast assumes the form of a tetrahedron, the nuclei lying near the corners. A depression appears in the center of each flattened surface, and the depression of each face is connected with that of each of the others by a furrow which bisects the edge of the tetrahedron across which it passes. These furrows may either take the form of a broad concavity with smooth curves, equaling in width about one half of the length of one edge of the tetrahedron, as is shown on the upper side of FIGURE 6; or they may be more abrupt, as indicated on the lower side of the same drawing. In no case was the inner edge of the furrow found to be sharp. In cells in which the protoplast has collapsed and shrunken into a smaller ball, the wall retains the form which it had at the time that the collapse occurred (FIG. 7). In such cases the appearance is as of ridges on the inner surface of the mother-cell-wall. The presence of these ridges in the fresh living material and their persistence, after plasmolysis has drawn the turgid protoplasm away, demonstrates that they are in no sense artifacts, or related to plasmolysis in any way, but that they actually occur in the division of the cell.

The furrowing of the plasma membrane and the simultaneous invagination of the mother-wall take place more rapidly at certain places than at others. It is evident that if there are four nuclei arranged tetrahedrally and equidistant from each other within a sphere, there will be four points upon the surface of that sphere which are equidistant from each of three of the nuclei. These points are the centers of the faces of the tetrahedron above described. By the transformation of the sphere into the tetrahedron the plasma membrane has been brought closer to the nuclear membrane. At these four points above mentioned on the plasma membrane the constriction of the mother-cell continues to proceed more rapidly than elsewhere. Thus there are formed four projections of the inner surface of the cell-wall which are equidistant from each other, one being in the center of each face of the tetrahedron, and which are connected with each other by a ridge of less magnitude. These projections, or invaginations, continue to elongate toward the center of the cell, and consequently in the direction of the fourth nucleus, keeping at all times equidistant from the three nuclei. As a result the four projections meet in the center of the tetranucleate cell, and fusion of their tips occurs (FIG. 8). Thus there are organized four protoplasmic masses each with a single nucleus and connected with each of the other four by an isthmus of cytoplasm, at first quite broad. It is evident that there would be six such isthmuses, not more than three of which would show in any one optical section.

Apparently each isthmus constricts independently of the others.

Many stages may be found showing different degrees of this constriction (FIGS. 9, 10, 12). The daughter-cells are not at first spherical. This may be related to the resistance of the thick mother-wall to transformation of form, or to the unequal rates at which the isthmuses narrow (FIG. 11). Upon the completion of the division each of the four cells is separated from each of the other three by a lateral wall which is thicker in its periphery and thinner at its center. Its form persists even after the protoplasts undergo plasmolysis (FIG. 13). Since in living cells the protoplast completely fills the space enclosed by the cell-wall, it will be seen that the daughter-cell is not perfectly spherical, but rather has in section the form of an ellipsoid. Such a condition is shown to the right in FIGURE 14. To the left, however, are cells which have proceeded a step farther and have approached the spherical form. Later (FIG. 15) the cells become exact spheres. This last change is accompanied by their enlargement and a decrease in thickness of the mother-cell-wall. The latter may involve a dissolution of the inner portion of the cell-wall. The entire cell does not retain its initial outline at this time, but assumes more nearly that of a tetrahedron; the division of the single spherical protoplast into four spherical protoplasts and the growth of the later has involved a considerable increase in the total volume, which has doubtless led to a stretching of the outer portion of the mother-wall. As the exine of the spores appears this mother-wall becomes thinner and thinner and finally disappears entirely.

From a study of the living material it has been shown that normally the mother-cell of *Nicotiana* thickens its walls during synapsis and the heterotypic karyokinesis, that no division of the cytoplasm occurs after the latter, but that the homoeotypic karyokinesis takes place almost immediately and is followed by a division of the tetranucleate cell into four uninucleate spores. This division involves a furrowing of the protoplast in the planes midway between the nuclei. It is not possible in the living material to determine the relation of cell to cell within the tissue, nor to study critically the details of the process of division.

V. THICKENING OF THE MOTHER-WALLS

In the fixed material it is found, as noted above, that the mother-wall begins to thicken during synapsis, commencing first at the corners, especially at the ends of the cell (FIG. 20). It is here thickened to a maximum degree of 1.4 microns, though the greater part of the thickened portion is about 1.05 microns in thickness. The mother-cells are arranged in the pollen chamber in general in two plates, lying side by side. The individual cells are usually elongated transversely to these plates, so that the one end of each mother-cell abuts upon the tapetal layer and the other upon the intercellular spaces between the two plates. It is as if the mother-cells mutually compressed each other, causing this modification of form, and permitting the thickening of the wall at first only at the points of least pressure.

In diakinesis the mother-wall is much more thickened. It may even reach a maximum of 7 microns, which is nearly as thick as it ever becomes. Usually, however, the thickened portion of the cell-wall in diakinesis has a maximum of about 4.2 microns, and its average thickness is about 2.8 to 3.5 microns. It is usually thickened throughout about one half of its area. In the early anaphases of the homoeotypic division the ends of the mother-cell are thickened to from 4 to 6 microns, and the lateral faces about 2 microns. The thickest portion of the wall at this time comprises about three fourths of its area. In the late telophases, however, the entire wall becomes almost uniformly thickened, so that it becomes difficult to determine the original longitudinal axis of the cell (FIGS. 24, 25). After re-organization of the daughter nuclei the wall appears thickened all around (FIG. 26), but there are variations in the degree of thickening which are not uniformly distributed. From the way the cells fit together in the pollen chamber it seems reasonable to conclude that the variations in thickness are related to the association of the mother-cells and their mutual pressure, etc., rather than to the composition of the mother-wall.

The absence of lamination or other visible differentiation in the mother-cell-wall indicates that the thickening process is not a growth by intussusception or apposition, but merely a swelling or gelatinization of the secondary strata of the mother-cell-wall. The wall appears perfectly homogeneous and stains a deep orange. A survey of the substances which stain orange in the cytoplasm leads one to the conclusion that they are often transitional forms of carbohydrates. Denniston (12) found an orange zone about the starch grains and attributed such a constitution to it. The orange zone which Timberlake found preceding the advent of the cell-plate is very likely composed of carbohydrate which was perhaps in the process of polymerization from a soluble sugar of low molecular weight through the less soluble dextrins, etc. and ultimately into cellulose. The orange-staining bodies in the cytoplasm of so many plant cells may possibly also be carbohydrate material of varying degrees of polymerization.

The history of the mother-cell-wall also indicates that during reduction it may be passing through transitional stages leading ultimately to its dissolution and disintegration. In most plant cells the mother-cell-wall persists after mitosis and becomes a part of the cell-wall of each daughter cell. The wall of the pollen-mother-cell, however, like that of other spore-bearing structures disappears as an entity, while the walls of the daughter cells are constructed entirely anew within the mother-cell. As has been shown above, the mother-wall beginning at the time of synapsis continues to thicken to a marked degree during the reduction divisions, and finally dissolves. It seems hardly possible that this thickening of the mother-cell-wall can be in the nature of growth, such as doubtless does occur in the formation of so permanent a structure as the exine, for example. Chemically considered this thickening of the mother-wall is probably in the nature of a colloidal swelling or hydration. Fischer (**19**) has recently attempted to demonstrate that hydration is not a stage in the process of solution as it has usually been considered. Though it may be that solution is not an absolutely necessary consequence of hydration, it is still true that very often, if not usually, solution does follow hydration. There is at least this much of a sequence in these cases; and solution involves a greater increase in colloidal dispersity than does hydration. It, therefore, does not seem illogical to conclude that the thickening of this mother-cell-wall is in the nature of an increase in colloidal dispersity of the substance of the wall, which process continues, and ultimately leads to such extreme dispersity that an entire dissolution of the mother-wall ensues. In addition to the cases of thickening of the mother-wall noted in the table below, Wille figures (**81**) this condition in 14 dicotyledons.

VI. THE CENTRAL SPINDLES

After the heterotypic karyokinesis the central spindle persists connecting the two daughter nuclei (FIG. 21). Fibers may be found running apparently the entire distance from one nucleus to the other; they are attenuated near their ends, giving the appearance of their being thickened throughout about one half or two thirds of their length in the central region. Careful examination, however, leads one to conclude that the fibers do not pull away from the nuclei. Scattered about in the cytoplasm are a few red-stained bodies, three of which are shown in the drawing. The hyaline area about each is probably an optical illusion due to diffraction. Comparison of this stage with a similar one in the dividing cells of the onion root-tip reveals the fact that in the latter the spindle fibers are somewhat more thickened throughout one half of their length in the central portion, and a very distinct orange zone and cell-plate have already begun to form in the equatorial region of the spindle. In the mother-cells of *Nicotiana*, however, no orange zone appears across the equator, and no blue-stained plate is developed. The fibers (FIG. 22) continue to become more arched, as the mother-cell approaches more and more the spherical form, and the rather rudimentary spindle takes on a more inflated aspect. The peripheral cytoplasm perhaps appears to be now more fibrillar; fibers run out from the nucleus in all directions to the plasma membrane and frequently cross along the surface of the spindle. There is no evidence that these crossing fibers become transformed into peripheral spindle fibers. In the later stages the fibers of the central spindle proper seem not infrequently to cross each other, whereas earlier (FIG. 21) such a condition was quite exceptional. It is difficult to state how this is brought about. There are apparently, however, many more fibers present in the cytoplasm in the later stages than immediately after the heterotypic karyokinesis.

The longitudinal axes of the homoeotypic spindles, as was observed from the study of living material, are frequently at right angles to each other (FIG. 23). By the time the metaphases of the second division have been reached, the heterotypic spindle has entirely disappeared. The cytoplasm presents a densely granular structure with evidence neither of alveoli nor of fibers;

the only kinoplasm present is the very distinct fibers of the spindles. The granules appear to be aggregated into more or less spherical groups (FIG. 24), which give almost a flocculent appearance to the cytoplasm. In addition there are scattered about many red-stained granules, which are about one eighth of the diameter of the chromosomes and have no special arrangement.

In the mother-cells of *Nicotiana*, when the daughter nuclei have become fully organized (FIG. 26), there is found a spindle between each pair of nuclei, that is, there are six spindles. These spindles are indistinguishable from each other, in other words it is not possible to tell either from the nuclei or from the spindles which of the four nuclei are sister nuclei. There must be then a disappearance of the homoeotypic spindles and the organization of six new spindles from the cytoplasm, or the former persist and there are organized four new spindles which are indistinguishable from them. As far as could be determined, the latter is the procedure in this form (FIGS. 24, 25).

Before the nuclear membranes are formed, the six spindles have become organized and are indistinguishable. The individual fibers are straight and parallel, the spindles not taking on the inflated appearance until about the time of the formation of the nuclear membranes. At first the fibers appear rather attenuate at their ends, as in the homoeotypic division; but very soon (FIG. 26) they are quite uniform throughout, at least there is no zonal differentiation. The fibers run from each nucleus to the others and to the plasma membrane as well. Were it not for the arching of the peripheral fibers of the spindle, it would almost seem as if the fibers radiate in all directions from the nuclei, and that the spindle is more or less an incidental and unavoidable consequence. It seems quite likely, however, that the spindle should be recognized as a special structure, though the other fibers, as far as the evidence goes, are of similar composition and character. In FIGURES 26, 27, and 28 the attempt was made to show all the fibers in the section, which was five microns in thickness, by changing the focus progressively during the course of making the drawing. A similar method was employed by Allen (1*b*) in his paper on *Polytrichum*. It will be seen that the fibers are attached to the nuclei more or less in bunches or tufts; from a single tuft there may proceed fibers both to the plasma membrane and to one or more nuclei. They rarely, if ever, run parallel or to the same region on another membrane. Quite regularly these tufts of fibers seem to be attached to the nuclear membrane just above the chromatic mass resulting from the transformation of a chromosome. These chromatic masses are practically all peripherally placed in the nucleus. It has been several times suggested that the material of the fibers is of nuclear origin, and this would indicate that the chromatin may have something to do with their formation or secretion from the nucleus.

VII. THE CONSTRICTION FURROWS AND NUCLEAR MIGRATION

In the tetranucleate pollen-mother-cell we have a condition which offers peculiar advantages for studies in nuclear migration, especially inasmuch as when first formed the nuclei are closely appressed to the plasma membrane (FIG. 26), whereas after spore-formation they lie in almost the exact center of the daughter cells. (FIG. 37). I have studied quite carefully the origin of the tetrahedral arrangement of the nuclei. It is by all means the prevailing arrangement in *Nicotiana*. In the examination of practically all of the hundreds of mother-cells in a single stamen, only four could be found which departed from this perceptibly, and none of these had a perfectly monoplanal disposition. The origin of the tetrahedral arrangement can not be attributed to the homoeotypic spindles, being from the first at right angles to each other. Probably in somewhat less than 50 per cent. of the mother-cells are they exactly at an angle of 90° during the anaphases. More often they have an inclination of from 45° to 60°. However, when the chromosomes have reached the poles, the four aggregates which they compose are found to be almost invariably equidistant, tetrahedrally arranged, and appressed to the plasma membrane (FIG. 25). It is thus just before nuclear re-organization that the tetrahedral arrangement is finally determined. Giesenhagen (24) has written extensively on the orientation of spindles and division planes, attributing them largely to the polarity of the mother-nucleus.

As noted, the cell was at first perfectly spherical, but soon the sides parallel with the spindles appear flattened (FIG. 27), the whole cell thus becoming a tetrahedron with each of its four faces lying over a group of three nuclei and parallel to the spindles between them.

At the middle of some of the spindle fibers at this stage there appear to be thickenings, but these little masses may also be found apparently unassociated with fibers. Occasionally one or two fibers nearer the center of the mother-cell may be found with a dense granular mass near its middle point. Such sporadic appearances are doubtless responsible for the statements by many authors that the division is of the ordinary cell-plate type; but there is no evidence that the fibers shorten at this time or at any time in the process of division. They are never seen to pull away from the nuclei and no plate or similar structure across the equator of the spindle is formed. The fixed material shows no plasmolysis in these stages, and the red, blue, and orange stains were well balanced. No difficulties in technique, such as Strasburger reports having encountered in the dicotyledons he studied, were here experienced. In a number of instances rows of granules were found; but these are as frequently, if not more often, located in other parts of the cell than the equatorial planes. Such a one may be seen in the upper left-hand corner of FIGURE 27, in the lower right-hand corner of FIGURE 28, in FIGURE 30, and in the lower left-hand corner of FIGURE 32. They are probably in most cases the result of chance distribution of granules, and only in three instances, FIGURES 27, 39, and 31, can they be considered as having any relation to cell-division. The last-named figure presents the nearest approach to a cell-plate which could be found. It might be argued that these rows of granules in various positions between the nuclei are composed of material which is diffusing from the nuclei to the plane of division, but no accumulation of such material in that plane in the form of a plate could be found.

A slight depression or concavity appears almost immediately (FIG. 27) in the plasma membrane at the equatorial plane of the spindle. At first it is rather abrupt, though the exact center of the concavity is always a smooth curve and never a sharp edge. Soon, however, this broadens into a wide smooth curve (FIG. 28), giving the mother-cell a lobed appearance. Spindle fibers may run to the plasma membrane in the region of the furrow, but there seems to be no tendency for them to be oriented thereupon any more than upon other points along the membrane. The spindles seem at this time to take on a little more definite organization. Not so many fibers are found crossing each other, and the individual spindles seem to be pressed together along the line where they are in contact, each one being thus quite definitely delimited. This results in many instances in the appearance of a triradiate figure composed of bundles of fibers (FIG. 28).

As the furrow deepens to the level of the outer margins of the nearest two nuclei it again becomes somewhat sharper. Meanwhile the nuclei slowly draw away from the plasma membrane (FIG. 29). The two edges of the furrow approximate an angle of 90° with each other, but the edge of the furrow is always rounded (FIG. 30). By this time the spindle has almost lost its inflated appearance. The peripheral fibers are no longer arched, as in the earlier stages.

The question as to the relation of the furrowing to the growth of the plasma membrane is a difficult one. It seems certain that growth of this membrane must take place at some time during the process of cell-division. It is not easy to determine whether the fibers are pushed before the invading membrane in the equatorial plane, as in animal cells, or whether the middle portions of the fibers as they successively come in contact with the invading membrane become absorbed in it, the remainder of the fiber between either nucleus and the new membrane persisting as radiating fibers. Such a transformation of fibers into plasma membrane would resemble that described by Harper (28*b*) for free cell formation in the ascus. The existence of such radiating fibers from the nucleus to the plasma membrane of the furrows may be found in all later stages of the division process (FIGS. 30–36). It seems not improbable that in *Nicotiana* also the spindle fibers are in part transformed into the plasma membrane. It is not, however, by any means proven that this is the only source of new plasma membrane material; but it is not surprising to find that here as well as in the cases where the cell-plate is the precursor of the plasma membrane, we may have the origin of that membrane from the fibers (kinoplasm) of the cell. As evidence accumulates it seems more and more likely that this kinoplasmic material arises from the region of the nucleus; this is then only further evidence that the material of the plasma membrane has its primary origin in the nucleus of the cell. The presence of radiating fibers from all sides of the nucleus to the plasma membrane, not only during division but as well in the young microspores both those of dicotyledons and of the larch, where in the latter case the division is by a cell-plate, makes the above interpretation possible whether it be assumed that the membrane grows by intussusception or apposition. There is no reason for presuming that the radiating fibers may not contribute to the growth of the plasma membrane as well as do the spindle fibers.

Considering the tetranucleate cell with the constriction furrows (FIG. 30) as a whole, it will be noted that inasmuch as there are six spindles, no two of which are parallel, there will be six furrows. Three of these furrows come together above each point of contiguity of three spindles. In other words, there are four points on the surface of the mother-cell at each of which three furrows meet. These points are the centers of the four faces of the tetrahedron. Each of these points of intersection is equidistant from the three nuclei, the mutual spindles of which are bisected by these furrows. Since the median line of each furrow is the arc of a circle which is smaller than a great circle of the tetranucleate cell, the points of deepest depression of these furrows are at their points of intersection, consequently there are four projections of the plasma membrane into the protoplast. Since the mother-cell-wall conforms to the plasma membrane exactly, the condition might be described as four equidistant invaginations of the mother-wall, each of which is connected with the others by a ridge upon the inner surface of the wall. These projections proceed gradually toward the center of the cell, keeping equidistant from the three nearest nuclei, and growing toward the fourth. It is thus apparent that these four projections finally meet in the center of the tetranucleate cell, before the furrows have completed the division in the equator of each spindle (FIG. 32).

The first indication of the growth of these projections toward the center of the mother-cell is in the straightening of the spindle fibers noted above (FIG. 30). This straightening results in the fibers pulling away from the center of the mother-cell, leaving a space which is triangular in section, but is really pyramidal, in the center of the cell. The eccentric position of the projection of the mother-wall shown in FIGURE 31 is not typical, and is doubtless due to the failure to cut all three spindles in the median plane, the one on the lower right side being cut near the periphery of the spindle. FIGURE 32 gives the typical condition. The projection of the mother-wall is triangular in section, the angles which are, however, never sharp, representing the edges of the furrows as they cut into the equator of the spindles. FIGURE 33 shows a section cut through the center of one of the nuclei of the mother-cell and tangential to two others, showing the projection of the mother-wall extending in to the center of the cell where it has fused with those from the three other directions.

By the fusion of the four projections of the mother-wall at the center of the mother-cell the latter is divided into four uninucleate protoplasmic masses, each connected with the other three by a broad isthmus of cytoplasm through which spindle fibers continue to pass. The furrows continue to deepen, as before, and the projection of the mother-wall enlarges transversely so that there is a constriction of the isthmus between each pair of daughter cells.

While these processes are going on, there is simultaneously a migration of the nuclei away from the plasma membrane (FIGS. 28–37); until at the end of the division the nucleus occupies the central position in the daughter cell. The conditioning factors in such migration have, of course, not yet been determined with certainty; it is, however, interesting to note that should the nuclei be thought of as bearing electric charges of like sign, they would behave as described: namely, assume a tetrahedral disposition before cell-division. And if further we think of the plasma membrane as bearing an electrical charge of sign unlike to that of the nuclei, the nuclei would ultimately move to a central position in the daughter cells, in other words to the position of equilibrium, considering that they bear charges unlike that of the plasma membrane.

The tetrahedral arrangement of the nuclei, and consequently of the microspores, seems to be the prevalent disposition among dicotyledons and, in fact, among all of the higher plants, especially those in which quadripartition has been found. Below is given a table, showing certain data on this point given in the literature. Of the forms studied in this investigation the predominant disposition in all is tetrahedral, though *Chrysanthemum* shows a greater diversity in this respect than any of the other species It will be seen that out of 50 forms of bryophytes, pteridophytes, and spermatophytes which have been studied in this respect, 40 are reported to have the tetrahedral arrangement; in only 19 have the nuclei been noted in the form of a rhomb or square; four forms occasionally show pyramids, and in three is found the arrangement in a single row. Of 42 forms which have quadripartition, 37 have the tetrahedral and 11 the rhomboidal or rectangular arrangement; none of these are reported to have the nuclei or spores arranged in a pyramid or row. It will thus be seen that the tetrahedral arrangement is by far the predominant, and the arrangement of the cells in pyramids or rows the most rare. The rhomboidal and rectangular disposition occupy intermediate relations, but the data have not been accurately enough recorded to determine which of these later is the more frequent. Hofmeister, Berthold, and Errera early contributed observations on the adjustment of the plasma membrane to Plateau's law of minimal surface; and Thompson (72) has recently called attention to this work, expressing the relation that (p. 424) "in a complex system of films . . . three partition-walls and no more meet at a crest, at equal angles." Harper (28*e*) in his study of *Gonium* colonies has laid particular stress upon the tendency of cells to group themselves in threes. He finds a tendency in the four-celled stage to shift from a rectangular monoplanal arrangement to that of a rhomb, wherein two of the cells opposite each other are closer together than the other pair, but in the older colonies the central four cells usually take the arrangement of a perfect square partly on account of the tension from the peripheral cells of the colony. This tension may be the consequence of the tendency for the peripheral cells to form groups of three with the central cells. The law of least surfaces certainly applies also to these mother-cells in quadripartition. It is evident that in the pyramidal arrangement of four spores in one plane there is one group of three, in the rhomboidal there are two groups of three, and in the tetrahedral there are four groups of three. It is apparent that if a surface be described about four spheres of equal size in such a way that it is tangential to the surface of the included spheres which are in contact with it, the extent of this described surface will vary with the arrangement of those spheres in the following descending order: linear, pyramidal, rectangular, rhomboidal, and tetrahedral. If then the mother-cell-wall is exerting a force of compression upon the four spores and the latter adhere closely together, we would expect to find the tetrahedral arrangement of the spores to be the most common. This is, of course, what we have observed above. But it should be remembered that the tetrahedral arrangement has been shown in *Nicotiana* to be determined, not during the division of the mother-cell, but previously near the close of the nuclear divisions. It is quite probable then that the restraining tension of the wall has very little to do with initiating the tetrahedral arrangement, though it may play a large part in the maintenance of such orientation. It is quite possible, as noted, that the appearance of the tetrahedral arrangement is to be attributed to a mutual repulsion between the daughter nuclei, and an attraction between them and the plasma membranes. It may be also that the movements of the plasma membrane in forming the furrow during cell-division, as described above, are in part at least an expression of this same force of attraction between it and the nuclei.

Each isthmus of the single mother-cell does not necessarily constrict at the same rate as the others (FIGS. 34, 35, 36). The division may, in fact, be entirely completed between two nuclei, before the isthmus between others has fairly begun to narrow. As the division proceeds the two sides of the same furrow come to lie more nearly parallel (FIG. 35), resulting in each of the daughter cells approaching more nearly to the spherical form. It is quite likely that this narrowing of the furrow is, in fact, to be attributed to the surface tension of the daughter cells. The portion of the surface of mother-cell over each nucleus, however, retains the form of an arc with a longer radius, indicating that the mother-wall is quite resistant to the rounding up process.

As division is completed, there is quite a definite system of radiating fibers in the cytoplasm (FIG. 36), running from the nuclear membrane to the plasma membrane and quite evenly distributed over the latter. Finally, however, the cytoplasm returns to the reticular appearance which it bore at the beginning of synapsis (FIG. 37), and the spores lie imbedded in the mother-cell-wall as a sort of matrix while the spore-coats are being developed.

VIII. OTHER DICOTYLEDONS

In the five other dicotyledons studied, the process of cytokinesis in the pollen-mother-cells was found to agree in all general particulars, as far as studied, with that in *Nicotiana*. In view of this fact, together with the large amount of collateral evidence presented in the review of the literature given, it seems quite probable that in a majority if not in all of the dicotyledons in which quadripartition of the pollen-mother-cells occurs, there is a division of the cytoplasm by constriction furrows, as above described for *Nicotiana*, without the development of a true cell-plate.

In *Helianthus* there is a greater number of blue-stained granules irregularly distributed throughout the cell at about the time of the beginning of the invagination of the mother-wall. They also frequently appear to be in chains, but these may lie either in or out of the equatorial plane. No evidence was found of these granules being arranged in the form of a plate. The same thickening of the wall occurs as in *Nicotiana*.

In *Chrysanthemum frutescens* a large number of irregularities occur as to number of pollen-grains formed from a single mother-cell. There sometimes appears to be only one, no division of the mother-nucleus taking place. In other cases, two, three, four, or five nuclei may be present and as many spores may be formed, respectively. When five are present they may all lie in one plane with one nucleus in the center and the other four at equal distances about it. In such cases there are eight spindles. The tetrahedral arrangement is, on the whole, less frequent in *Chrysanthemum* than in *Nicotiana*. The size of the respective nuclei in the mother-cell also varies. Sometimes it appears as if a nucleus was organized from a single chromosome, and several instances of very small pollen-grains have suggested that these might be later stages of such an aberrant development as Juel found was the case in *Hemerocallis*. A study of nuclear division in *Chrysanthemum* would doubtless lead to interesting results. The cell-division of the pollen-mother-cells appears to be as described above for *Nicotiana*. This last statement may also be made for the other member of the Compositae that was studied, namely *Ambrosia artemisiifolia*.

The author is able to confirm the statement of Miss Digby that constriction occurs in *Primula*. No evidence of a cell-plate was found. The isthmus between the nuclei in the later stages takes the form of a narrow neck, the daughter cells being farther apart than in *Nicotiana*. With regard to *Tropaeolum*, mother-cells were found which confirmed the figures of Strasburger with respect to the row of granules in the equatorial plane; but rarely, if ever, were they as prominent as his drawings show them, and they are arranged in chains and not in a plate. Furthermore, other mother-cells were found which contained no such chain of granules, or, if one was present, it lay in another part of the cell. The hourglass-like figures which appear in *Primula* were also noted in *Tropaeolum*. No evidence of a true cell-plate was found.

There is in these pollen-mother-cells no indication of a centrifugally formed continuous cell-plate such as is so conspicuous in the pollen-mother-cells of the lily and the larch and in vegetative cells of the higher plants. The central spindle is poorly developed and there is no shortening of its fibers. But the fact that we have here, as in cell-plate formation, the close association of the fibers with the formation of the plasma membrane, points to the importance of the study of these structures in their relation to the phenomena of cell-division.

Further studies are contemplated, involving a wide range of species and extending to the nuclear phenomena incident to quadripartition.

IX. Discussion

The existence of a form of division by furrowing in certain cells of the higher plants suggests the possibility of ultimately harmonizing the usual division by cell-plates in these forms with the division by so-called constriction in the higher animals. As noted above, there are in the lower plants and animals also types of cell-division more or less intermediate between these two extremes; and it seems highly probable that the processes involved in these essential phenomena of cellular reproduction are determined by the fundamental physico-chemical properties of the complex colloidal protoplasmic mass. The fact that in many cases of quadripartition, as described above, there is a gelatinization of the cell-wall just prior to the division of the cell by furrows indicates that the cell-wall may be an important factor in controlling such form changes as occur in division by furrows. This only emphasizes the contention that botanists have no right to consider the protoplast alone as the cell. The growing and dividing cell of the higher plants should be thought of as a unit comprised both of protoplast and cell-wall. It is certainly a striking fact that these pollen-mother-cells whose walls become a gelatinous matrix, like that present in so many animal cells, especially eggs, and whose protoplasts assume a spherical form like the egg cells of many animals, divide in a fashion quite analogous to that of the latter: namely, by a centripetal furrowing of the cytoplasm without the formation of a cell-plate.

The occurrence of the various types of division of the spore-mother-cells of the higher plants, as shown by the data thus far accumulated in the literature, is indicated in the following table. It must constantly be remembered that much of it is introduced incidentally to other investigations and is based on fragmentary evidence. With this in mind the evidence as to quadripartition, arrangement of spores, and thickening of the wall, presented by the early cytologists, who had these things definitely in mind, are quite as dependable as the isolated statements of more recent workers.

Cell division in mother-cells

PLANT	ARRANGEMENT	PARTITION	DIVISION BY	AUTHOR	MOTHER-WALL
Aneura	tetrahedral	bi-	cell-plates	Farmer & Moore	
"	"	quadri-	" "	Farmer	
Pellia	"	bi-	" "	"	thick
"	"	quadri-	" "	Strasburger	
Fegatella	rhomb	"	" "	Farmer	
Pallavicinia	tetrahedral	"	" "	"	
Anthoceros	"	"	furrowing	Hofmeister	
"	"	"	cell-plates	Strasburger	
"	"	"	(?)	Davis	
Funaria	"	"		Sachs	
Pteris	"	"	cell-plates	Calkins	
Osmunda	"	"	" "	Smith	
Botrychium	"	"	" "	Stevens	thin
"	monoplanal	"	" "	"	"
Polypodium	"			Russow	
Equisetum	tetrahedral	quadri-		Russow	
"		bi-	furrowing	Hofmeister	
"	tetrahedral	quadri-	cell-plates	Strasburger	thick
"	monoplanal	"	" "	"	"
Psilotum		bi-	" "	"	
"	monoplanal		furrowing	Hofmeister	
Isoetes	tetrahedral	quadri-	cell-plates	Strasburger	thick
Marsilea	"	"	(?)	"	"
"	monoplanal	"	(?)	"	"
Ceratozamia	"	bi-	furrow. cell-plates	Jurányi	"
"	tetrahedral	"	furrow.	"	"

PLANT	ARRANGEMENT	PARTITION	DIVISION BY cell-plates	AUTHOR	MOTHER-WALL
Zamia	"	"	cell-plates	Treub	"
"	monoplanal	"	" "	"	"
Pinus				Hofmeister	
Larix	tetrahedral	bi-	cell-plates	Timberlake	thin
"	"	quadri-	" "	"	
"	monoplanal	bi-	" "	"	
			Monocotyledons		
Allium		bi-	cell-plates	Pringsheim	thick
Tradescantia		"	" "	Hofmeister	
Fritillaria, Lilium,		"	" "	Strasburger	
Anthericum		"	" "	"	
Funkia		"	" "	Sachs	
Potamogeton,		"	" "	Wiegand	
Convallaria		"	" "	"	
Symplocarpus,		"	" "	Duggar	
Peltandra		"	" "	"	
Trillium		"	" "	Atkinson	
Agave		"	" "	Schaffner	
Zea		"	furrowing	Kuwada	
Musa	tetrahedral	"	(?)	Tischler	
"	rhomb, row,		(?)	"	
"	square, etc.	"	(?)	"	
Neottia		"	no cell-plates	Hofmeister	
Orchis		"	" " "	"	
Cypripedium		"		Guignard	
Epilobium			cell-plates and furrowing	Tschistiakoff	
Carex			cell-plates	Juel	
Hemerocallis		incomplete	" "	"	
Naias		quadri-		Hofmeister	
Iris		"	furrowing	"	thick
Orchids	monoplanal	"	cell-plates	Guignard	
Sisyrinchium	tetrahedral	"		"	thick
Aloe, Ixia, Freesia,		"		"	
Apicra		"		"	
Monbretia, Gasteria,		"		"	
Haworthia		"		"	
Asphodelus		"		Strasburger	
Epipactis		bi-	cell-plates	Wille	medium
Potamogeton	pyramid			"	"
			Dicotyledons		
Asclepias	row	bi-	cell-plates	Strasburger	thin
Ceratophyllum	tetrahedral	"	" "	"	"
"	monoplanal	"	" "	"	"
Rafflesia	tetrahedral	"	" "	Ernst & Schmidt	
"	monoplanal	"	" "	" "	

PLANT	ARRANGEMENT	PARTITION	DIVISION BY	AUTHOR	MOTHER-WALL
Apocynum	row, pyramid, square	"	" "	Frye & Blodgett	
"	rhomb, tetrahedral	"	" "	" "	
Passiflora		bi-	cell-plates	Hofmeister	
Taraxacum		"	(?)	Osawa	thick
Hieracium		"	(?)	Rosenberg	
Momordica		"		Wimmel	
Mirabilis		"		Tischler	thick
Aristolochia	square, pyramid	"		Samuelsson	
Acacia		"	no cell-plates	Rosanoff	
Lathyrus		"	furrowing	Gregory	
Nymphaea	tetrahedral	quadri-	(?) cell-plates	Lubimenko & Maige	
Podophyllum	rhomb	"	" "	Mottier	
Syringa		"	" "	Juel	
Bignonia		"	" "	Duggar	
Lavatera	rhomb	"	" "	Byxbee	thick
Cobaea	tetrahedral	"	" "	Lawson	thin
Cucumis	tetrahedral	"	" "	Strasburger	thick
Cucurbita, Bryonia	"	"	(?)	Naegeli	"
Oenothera		"	cell-plates	Gates	
"	tetrahedral	"	(?)	Naegeli	thick
"		"	furrowing	Beer	
Althaea		"	cell-plates at times	von Mohl	
"			cell-plates	Wimmel	thick
"	tetrahedral	quadri-	(?)	Pringsheim	"
"	square	"	(?)	"	"
Tropaeolum	tetrahedral	"	cell-plates	Strasburger	"
"		"	cell-plates and furrowing	Sachs	
"	tetrahedral	"	furrowing	(see above)	thick
Ribes	tetrahedral, rhomb	"		Tischler	
Hesperis, Pisum			no cell-plates	Baranetzky	
Lathyrus, Ipomoea			" " "	"	
Dahlia	tetrahedral	quadri-	" " "	Ishakawa	
Drosera	rhomb, tetrahedral	"	(?)	Rosenberg	thick
Hieracium	monoplanal	"	(?)	"	thin
Daphne	tetrahedral	"	(?)	Osawa	
Taraxacum	"	"	(?)	"	
Convolvulus		"	furrowing	Wimmel	thick
Houttuynia		"	"	Shibata & Miyake	
Passiflora		"	"	Hofmeister	thick
Vicia	tetrahedral	"	"	Fraser	
Primula	"	"	"	Digby	thick
"	"	"	"	(see above)	"

PLANE	ARRANGEMENT	PARTITION	DIVISION BY	AUTHOR	MOTHER-WALL
Sarracenia	"	"	"	Nichols	
Gossypium		"	"	Cannon	
Crepis	tetrahedral	"	"	Beer	thick
Hamamelis	"	"	"	Shoemaker	"
Parnassia	"	"	"	Pace	"
Nicotiana	rhomb, tetrahedral	"	"	(see above)	"
Chrysanthemum	tetrahedral	"	"	" "	"
Ambrosia	"	"	"	" "	"
Helianthus	"	"	"	" "	"

It will thus be seen that quadripartition has been reported in, at least, 32 dicotyledons, 11 monocotyledons, 1 gymnosperm, 6 ferns, 1 moss, and 5 liverworts. Bipartition in the spore-mother-cells has also been reported in each of these groups, except the mosses; but only 12 cases are noted in dicotyledons, and 18 in monocotyledons. Quadripartition by cell-plate formation has been reported most abundantly in the liverworts, due largely to the work of Farmer, and in the ferns. Nine cases have been reported among the dicotyledons; they are: in *Oenothera* by Gates, in *Podophyllum* by Mottier, in *Syringa* by Juel, in *Lavatera* by Byxbee, in *Cobaea* by Lawson, in *Bignonia* by Duggar, in *Althaea* by von Mohl and by Wimmel, and in *Cucumis* and *Tropaeolum* by Strasburger. The statements by the writers of some of these papers as to the presence of a cell-plate have been seriously brought into question by more recent work on the same plants. The other papers give no figures which in any way demonstrate the presence of a cell-plate in these divisions. Their evidence consists entirely of statements without confirmatory description or figures, and in view of my results on *Nicotiana* can not be accepted as final evidence. On the other hand, there is more or less evidence that quadripartition occurs by furrowing and without a cell-plate in 21 dicotyledons. In 18 dicotyledons quadripartition is reported as accompanied by a thickening of the mother-wall. In none of these has a cell-plate been demonstrated beyond doubt. In fact, no case has been proven in any plant, so far as the present survey of the literature goes, in which quadripartition by cell-plates has been found in a cell with a greatly thickened mother-wall. The nearest approach to this is given in Strasburger's

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[1] The data in the last column are based upon the authors' drawings respectively, measuring from the outer boundary of the cell wall to the protoplast.

study of *Equisetum* and *Isoetes*, done at the same time as that on *Tropaeolum*, and presenting the same evidence, which in the light of the observations recorded above, must be regarded as doubtful.

We are forced to conclude with Guignard then, as against Dippel, Samuelsson, and others, that quadripartition and bipartition may occur in either monocotyledons or dicotyledons. Furthermore, there is no doubt that cell-plates occur in the bipartition of the pollen-mother-cells as well as the vegetative cells in both monocotyledons and dicotyledons. We have seen that the wall of the pollen-mother-cell may be thickened in members of either one of these groups. So that there seems to be no evidence that these two groups of flowering plants differ in general in any way in their mode of microspore formation.

Since so little is known of the dynamics of cell-activities of any kind it is very difficult even to attack the question as to what physico-chemical processes are involved in cell-division. However, it is to be hoped that the discovery of a closer relation between the two diverse types of cell-division: that by furrowing, characteristic chiefly of animal cells, and that by cell-plate, common to higher plants, will help to bring to view a new standpoint from which the physiological processes of cell-division may be more effectively studied.

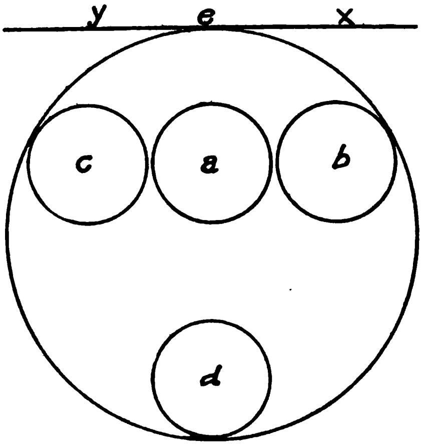
The almost infinite complexity of protoplasm has been so often emphasized that it need not be further mentioned here. In addition to the great variety of chemical compounds in the cell, these exist in all sorts of physical states. There are particles in suspension, and substances in true solution; and between these two extremes there are substances in all possible degrees of dispersity, including suspensoids and emulsoids, making up the colloidal mass of protoplasm. Not only is there an almost infinite complexity, but the material is in a constant state of flux.

In describing above my observations on the migration of nuclei, it was suggested that the nuclei move about in the mother-cell as if they all bore electrical charges of like sign while the plasma membrane bore charges of opposite sign. The location of electrical charges on the membranes of the cell seems quite probable from the standpoint of recent developments in physical chemistry. According to the Gibbs-Thomson principle, there is a tendency for substances to accumulate upon surfaces. It is practically certain that the ions of many inorganic salts are to be found within the cell, and these are known to have a relatively high speed of diffusion, and hence might be thought of as accumulating upon the membranes of the cell. If, as there is some evidence to indicate, the plasma membrane is colloidal and if it may be inferred that the same is true of the nuclear membrane, this colloidal condition would serve to increase very much the amount of ionic material which might be adsorbed upon the membranes. It is not difficult then to see how great numbers of ions might accumulate there, and if they are of like sign they would give to that membrane an electric charge.

If, for example, the nuclear sap were markedly acid and the cytoplasm be markedly alkaline, there will accumulate upon the plasma membrane charges of one sign, while upon the nuclear membrane there will accumulate predominately charges of the opposite sign. It seems thus possible from a physico-chemical standpoint that such membranes may have acquired opposite charges. But for the purpose of this discussion, it makes no difference how these membranes may have received their charges; it is simply proposed to show that they, at least at certain stages, behave as if so charged.

As noted above, the nuclei of like charge would repel each other and hence take up a tetrahedral arrangement within the cell. The charges upon the plasma membrane and nuclear membranes would not necessarily be neutralized by contact of the membranes since the ions are adsorbed.

The mutual repulsion of the nuclei and their attraction for the plasma membrane opposed by the repulsion between different areas of the plasma membrane will tend to transform the perfect sphere into a tetrahedron with four equal triangular faces, each parallel to the plane of three of the nuclei. Now the center of each of these triangular faces will be attracted equally by each of these three nuclei and also to some degree by the fourth. The resultant of these four forces will tend to draw this point toward this fourth nucleus; and the latter will exert relatively more force of attraction upon this point than any one of the other three nuclei; for, though it is farther away, it is working in the direction along which the point will move. This portion of the plasma membrane will tend to move toward the fourth nucleus, that is, toward the center of the cell, and there will thus be formed an invagination or projection of the plasma membrane from the center of each of its triangular faces toward the center of the cell. Now let the accompanying diagram represent the cell at the stage just described:



TEXT-FIGURE 1. Diagram of mother-cell before division.

Let *a*, *b*, *c*, and *d* be the four nuclei, and let *e* be a point on the plasma membrane equidistant from *a*, *b*, and *c*. The cell is shown in its three dimensions, and these must be kept in mind during the discussion. Two of the four nuclei, *a* and *c*, are on either side of the plane of the diagram. Let *xy* be a plane tangential to the plasma membrane at the point *e*, and let *x* be the point of intersection of the perpendicular dropped from *b* to the plane *xy*. By actual measurement of the cells, *ed* is about 16 microns, *cb* is 14 microns, and *xb* is 7 microns. Now if there is an attraction between each of the nuclei and the point *e*, this point would tend to move along the line *ed*. Let *EB* represent the force exerted by *b* to draw *e* along the line *ed*. Then the force exerted by *a* and *c* respectively would also be equal to *EB;* therefore the total force exerted by the three nuclei, *a*, *b*, and *c* will be 3*EB*. Let *EB* represent the force exerted by *b*. The force exerted by *a* and *c* respectively will also be *EB*. Now the angle *xeb* may be shown geometrically to be one-half of a right angle. Therefore the resultant of the forces exerted by the three nuclei, *a*, *b*, and *c*, will be about 2*EB*. Now *ed* is less than 2*eb*, and therefore, since the force is inversely proportional to the square of the distance, the actual force exerted by *d* would be less than *EB*. As *e* approaches *d* this force would be much greater, whereas the force resulting from the attraction of *a*, *b*, and *c* would diminish. The resultant of forces in the early part of the process would be about 3*EB*. But in a binucleate cell the resultant of forces which would operate to draw the plasma membrane along the equatorial plane would be the sum of the attracting forces of only two nuclei, each in such a relation as *b* to *e*. It thus appears that the resultant of forces in a binucleate cell would be less than those in a tetranucleate cell.

When the furrow is formed, the nucleus is more nearly enveloped by the plasma membrane and hence the position of equilibrium, on the basis of the electrical charges postulated above, would be nearer the center of the lobes. And when constriction is complete we should find the nucleus in the exact center of the daughter cell. It is to be borne in mind, of course, that the furrows as they come nearer and nearer together, being of like sign will repel each other. Also the opposite surfaces of the same furrow as it grows deeper and deeper will more and more repel each other. The problem almost immediately becomes too complex for analysis in the present condition of our knowledge as to the actual distribution of the ions in the cell solutions and on its membranes. I have merely endeavored to point out certain possibilities as to the distribution of the forces concerned in initiating cell-division by the process of constriction. While it is not contended that these electrical charges are the only factors in the division of the cells, yet it is interesting to note that both the nuclear and plasma membranes behave in the initial stages of division as if so charged.

It is quite likely that the thickened mother-wall exerts no unevenly distributed force of compression upon the protoplast while in the spherical form. The tetrahedral arrangement of the spores has been shown to have originated in the migration of the nuclei when the mother-cell was spherical in form, hence it is not necessary to postulate the cell-wall as the determining factor in the accomodation to least surfaces, which is effected by the tetrahedral arrangement. Furthermore, the surface tension of the protoplast may be well thought to operate to bring about this result. The mother-wall seems to behave as if it were a plastic, more or less gelatinous, substance with some elasticity, so that it would offer little or no resistance to changes in form of the cell within. The mother-cell then as soon as the mutual pressure of other cells is removed, assumes the form of least surface, doubtless due to cell-turgor and surface tension.

It seems entirely probable that the cellulose wall of the typical plant cell exerts much more opposition to changes in the form of the protoplast, and has a restraining effect against an increase in volume. But whether the typical cell-wall of plants has a high or low degree of elasticity, we must conclude that these mother-cells with their spherical form and loose arrangement in the pollen-chamber are free to undergo such changes in volume and form as their internal constitution will favor. The pollen-mother-cell thus approaches the condition which is found in the egg cells of many animals, and it is quite suggestive that we should here find a mode of cell-division quite like that in the latter. Whether we shall be able to explain this division in plants on the basis of surface tension, as Robertson and McClendon have attempted in animal cells, is perhaps a question. But it is clear that such factors as surface tension, osmosis, and electrostatic equilibrium are involved and their relation to the process must be considered.

It may be that this close approach in the quadripartition of pollen-mother-cells to the animal type of cell-division may throw some light on the nature of the cell-plate. It is possible that in all cell-divisions, animal and plant alike, there are fundamental conditions tending to cell-plate formation, and that in the majority of the cells of higher plants alone do we have the full complement of factors necessary for the expression of these conditions in the form of a visible structure. The ability of these pollen-mother-cells to enlarge to a point of equilibrium between osmotic pressure and surface tension may present conditions favorable for the process of anatonose, as Errera termed it, in which soluble substances are formed in the equatorial plane. In the ordinary tissue cells of the higher plants, the retentive cell-wall and adjacent cells may make such enlargement impossible so that katatonose occurs and a coagulation or precipitation of a compound organic salt, takes place in the region of the equator. The relation of the spindle fibers to cell-plate formation, and the relation of the former to the nuclei, favors the idea that the cell-plate is primarily of nuclear origin. It is not unthinkable that in all cases complex or simple unsatisfied soluble ions may diffuse outward in all directions from the nuclei, possibly streaming along the paths in the colloidal protoplasm marked by the fibers.. The ions from different nuclei would meet in an equatorial plane and might, if conditions admit, form an undissolved compound. If, however, the cell was able to admit water and increase in volume in response to the increased osmotic pressure, these salts might remain at a concentration below the saturation point and hence not precipitate. May it not be that such a condition exists in these mother-cells, which are able to increase their volume considerably? On this interpretation there would be in these mother-cells an invisible cell-plate of soluble material, and the relation of division by furrows to that of the ordinary type of higher plants becomes more comprehensible.

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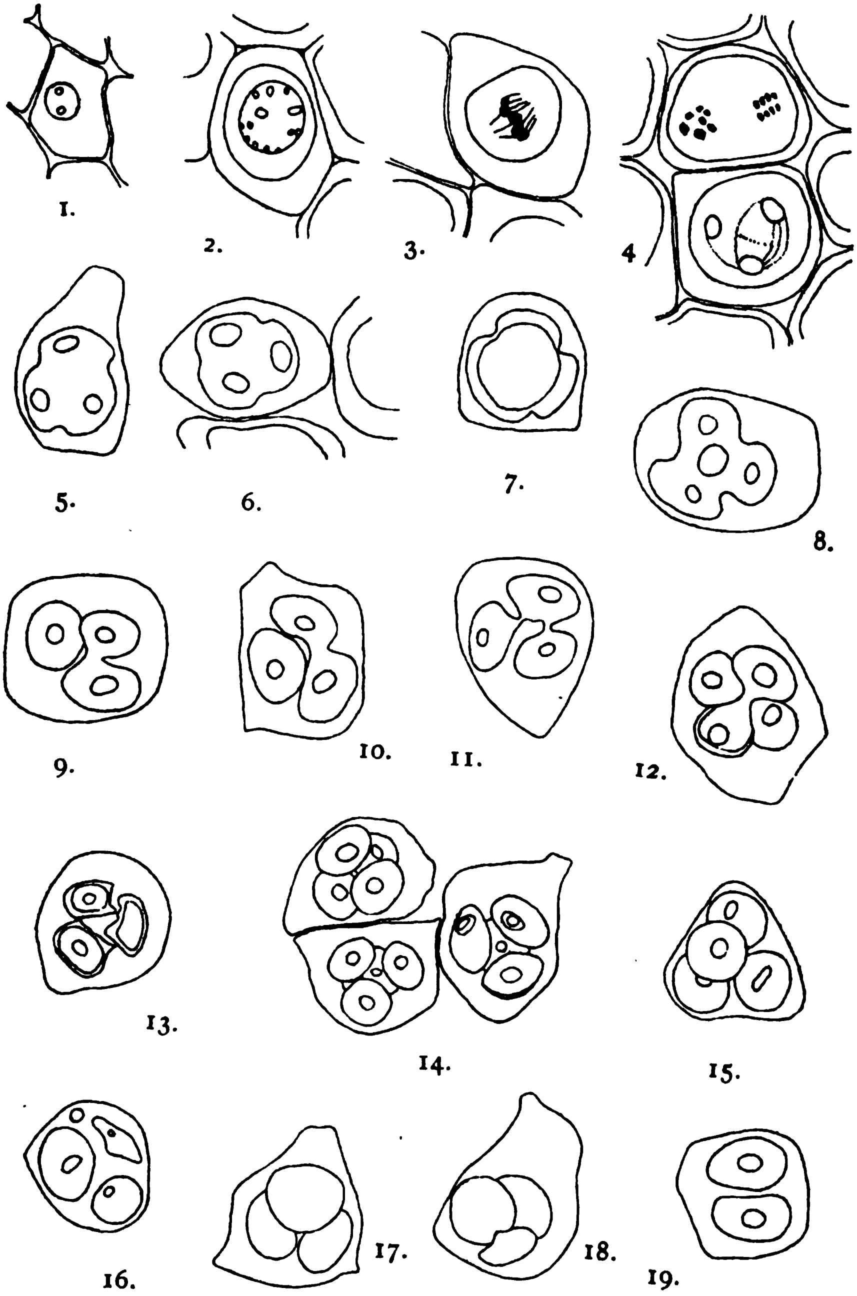
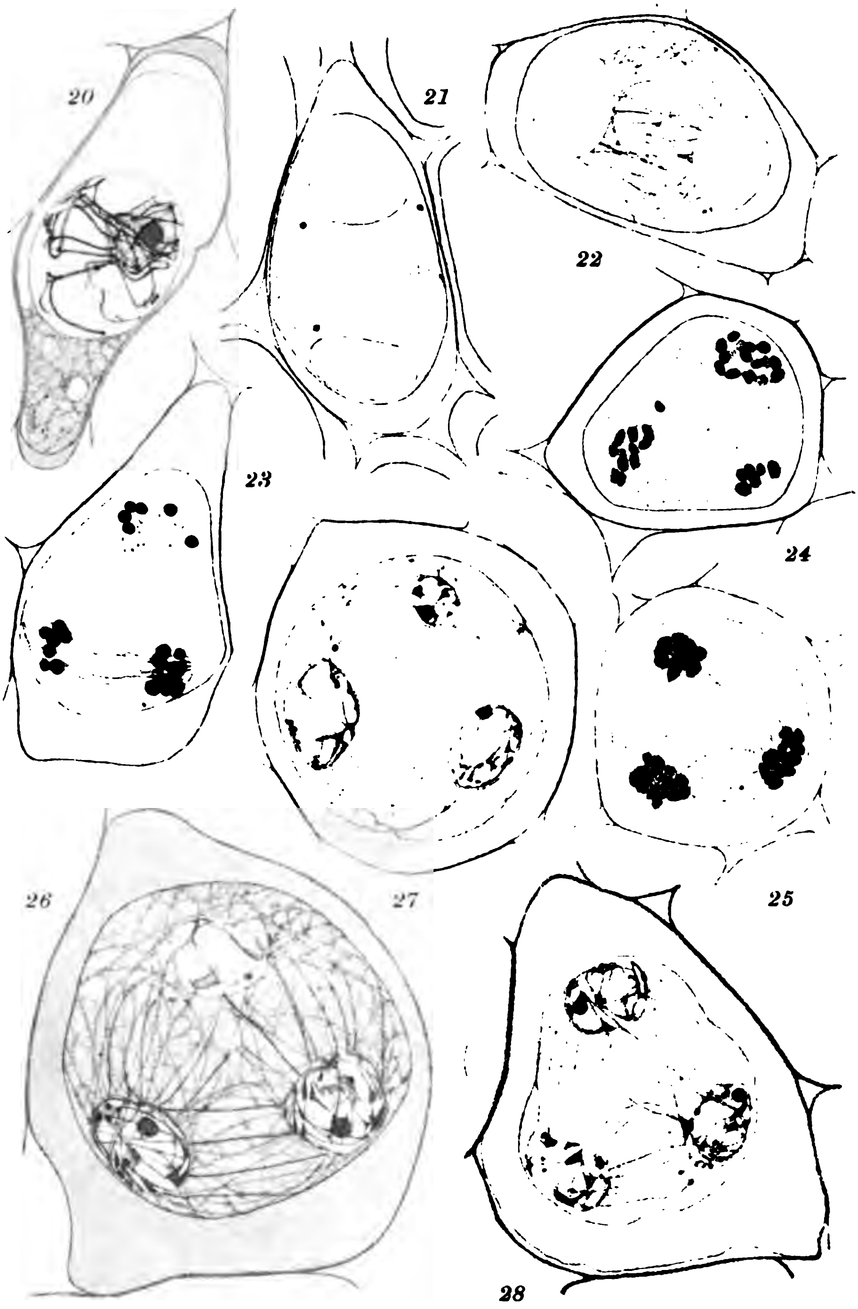
XI. Explanation of plates 27–29

The accompanying drawings were made with a Leitz one-sixteenth objective, Apert. 1.32, and ocular, number 3, with a tube length of 15. The cells are magnified about 1000 times in figures 1 to 19 inclusive, which are of living cells of *Nicotiana*. The fixed cells of *Nicotiana*, figures 20 to 37 inclusive, were drawn about 1875 times their actual size.

1. Mother-cell in presynapsis.
2. Diakinesis, wall thickened.
3. Equatorial plate stage of heterotypic karyokinesis.
4. Anaphase and telophase of homoeotypic mitosis.
5. Furrows which divide mother-cell just appearing.
6. Similar stage, showing large intercellular spaces.
7. Similar stage, with content plasmolysized to show ridges on wall.
8. Furrows well developed, and having invaded the center of the cell.
9. Isthmus becoming quite narrow.
10. Another cell in similar stage.
11. Isthmus having become very narrow.
12. Similar stage.
13. Division complete, cell plasmolyzed to show form ot cross-wall.
14. Division complete, spores changing from an elliptical to a spherical form.
15. Spores become perfect spheres, mother-wall becomes thinner.
16. Four spores of unequal size, within the mother-wall.
17. Three spores of equal size within the mother-wall.
18. Two large and one small spore within the mother-wall.
19. Two spores within the mother-wall.
20. Synapsis, showing wall thickened at ends of cell, and middle lamella.
21. After heterotypic karyokinesis, ends of fibers attenuated.
22. A little later, spindle inflated, wall thickening.

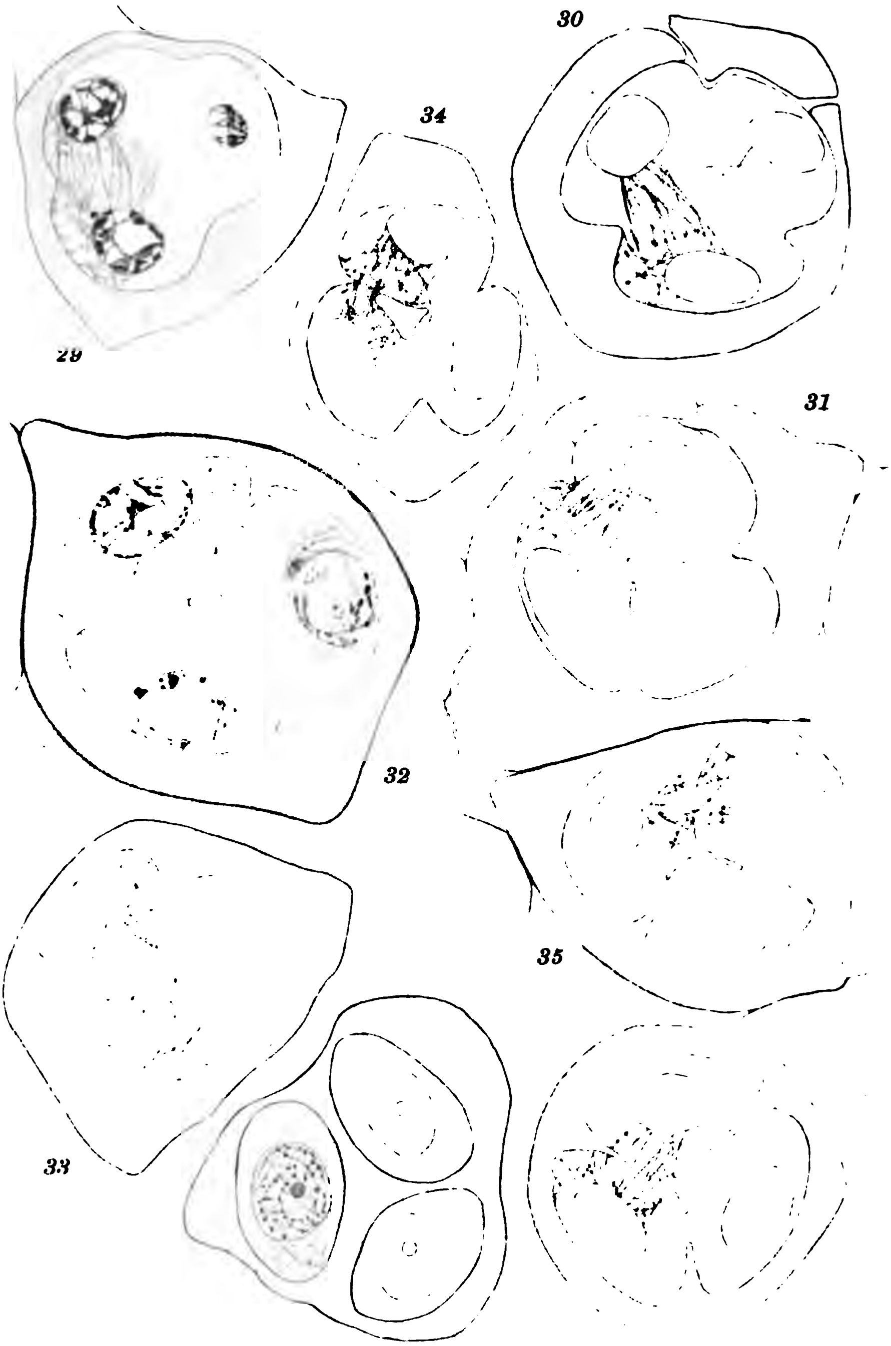


FARR: CYTOKINESIS OF POLLEN-MOTHER-CELLS



HELIOTYPE CO., BOSTON

FARR: CYTOKINESIS OF POLLEN-MOTHER-CELLS



HELIOTYPE CO., BOSTON

FARR: CYTOKINESIS OF POLLEN-MOTHER-CELLS

23. Anaphase of homoeotypic, spindles nearly at right angles, cytoplasm not shown.

24. Early telophase, cytoplasm granular, wall uniformly thickened.

25. A little later, cell spherical, spindles appearing, peripheral cytoplasm not shown.

26. Nuclei organized, cytoplasm fibrous, wall much thickened, surface only of upper nucleus shown.

27. First indication of cell-division, upper nucleus not shown in central section.

28. Sides of mother-wall becoming concave, spindles distinct.

29. Furrows deepen, nuclei draw away from the membrane.

30. Spindle fibers straighten, and draw away from the center of the cell.

31. Furrows become more abrupt.

32. Projections of the mother-wall reach the center of the cell, all three nuclei shown in central section.

33. Tangential to two nuclei, showing the invagination of the cell-wall.

34. Unequal narrowing of isthmuses.

35. Furrows sharpen, and daughter cells begin to round up.

36. Division complete at one isthmus, before the others.

37. Spores distinct and imbedded in the thickened mother-wall, cytoplasm alveolar.

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